

MIDDLE ORDOVICIAN BIVALVES FROM SPAIN AND THEIR PHYLETIC AND PALAEOGEOGRAPHIC SIGNIFICANCE

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ABSTRACT. The rich bivalve fauna from the Middle Ordovician of Spain is reviewed, and some new taxa established: *Dulcineaia manchegana* gen. and sp. nov., *Praenucula sharpei* sp. nov. and *Ekaterodonta hesperica* sp. nov. Some palaeotaxodontids probably had archaic characters, such as the dentition of *Ekaterodonta* and the pedal muscles of *Myoplusia*. The common trend towards the production of crenulated teeth among actinodonts and their descendants is underlined; *Dulcineaia* is a new example among Redoniidae. The comparison with the crenulations of some palaeotaxodontids does not show any general constraints governing the evolution of microcrenulations. Bivalve distribution within the *Selenopeltis* province is apparently complex with some endemics during the Middle Ordovician. The Spanish faunas were largely dominated by small endobenthic shells which suggests a cool-water area.

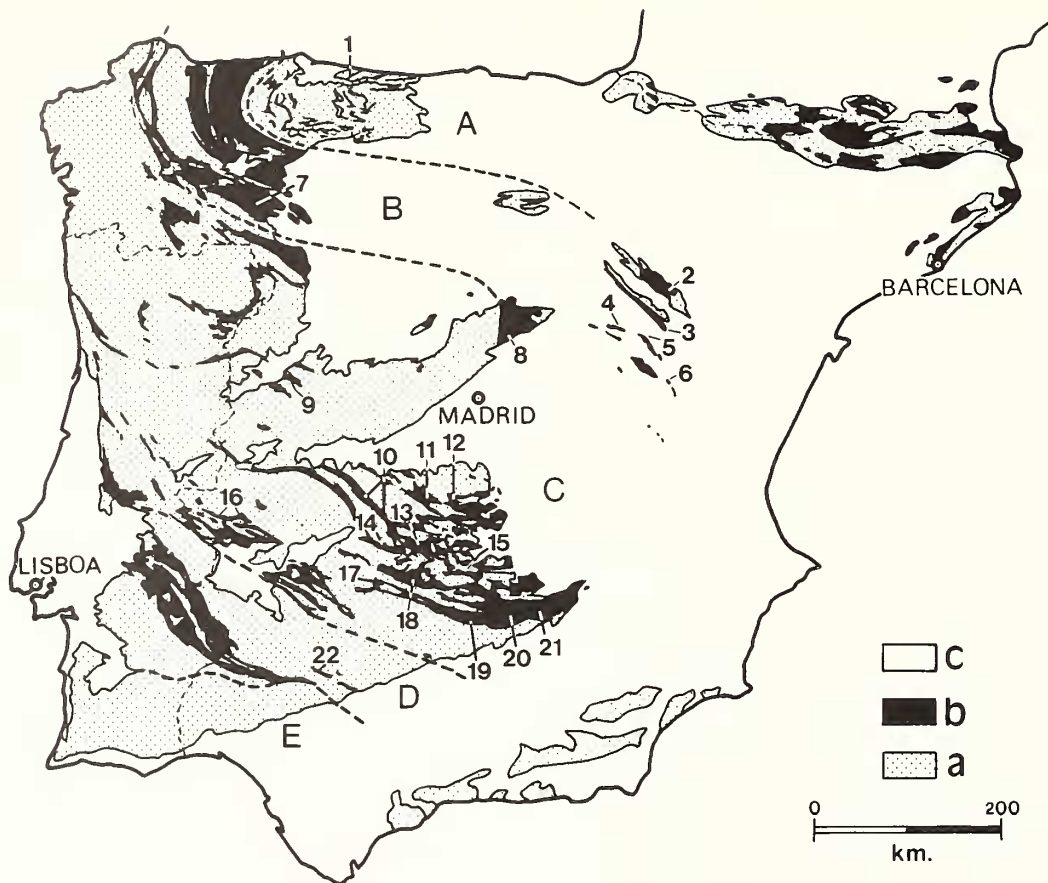
THE Middle Ordovician bivalve molluscs from the shales of the Hesperian Massif were described by Sharpe (1853) from Portugal and by de Verneuil and Barrande (1856) from Spain. Since then, these faunas have not been revised. In contrast, other groups, trilobites, graptolites, echinoderms, have provided the basis of numerous studies which have enabled a precise biostratigraphy for the Llanvirn and Llandeilo series to be established in the Hesperian Massif (Hamman 1974, 1983; Hamman *et al.* 1982; Romano 1982; Gutiérrez-Marco *et al.* 1984*b*; Rábano 1984, 1988; Gutiérrez-Marco 1986). The only indications of bivalves are a list of species by Gutiérrez-Marco *et al.* (1984*b*), a figure of *Redonia* cf. *deshayesi* from the Ossa Morena Zone (Gutiérrez-Marco *et al.*, 1984*a*) and the description of a new cycloconchid (Babin and Gutiérrez-Marco 1985). Similar faunas have been the subject of detailed researches in the Armorican Massif (Babin 1966, 1977; Bradshaw 1970). Increasing interest has been given to other Lower and Middle Ordovician bivalve faunas elsewhere (Pojeta 1971; Morris and Fortey 1976; Pojeta and Gilbert-Tomlinson 1977; Pojeta 1978; Morris 1978, 1980; Babin 1981, 1982; Babin *et al.* 1982). Thus, it is appropriate to revise the systematics of these numerous and diverse molluscs in a modern framework, and to discuss their phyletic and palaeogeographical significance.

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GEOLOGICAL SETTING OF SPANISH MIDDLE ORDOVICIAN BIVALVES

We have studied 2400 bivalve samples from 87 localities widely distributed along the Spanish part of the Hesperian Massif. This massif comprises a large area of the Iberian Peninsula and contains the most extensive outcrops of Ordovician rocks known in the European Hercynian fold belt. Text-figure 1 shows the approximate position of the fossil localities. Their detailed locations have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14041 [6 pages].

The bivalve faunas come from several formations, composed mainly of shales with scarce sandstones, the latter predominating only in the youngest beds of the succession. They can all be assigned to the 'Tristani Beds' of early authors, which have been divided into a number of



TEXT-FIG. 1. Map showing outcrops of Ordovician rocks in the Iberian Peninsula in solid black with the studied Lower Ordovician bivalve localities. Symbols: a, Precambrian and Palaeozoic rocks; b, Ordovician outcrops; c, post-Palaeozoic cover. A-E, structural zones of the Hesperian Massif: A, Cantabrian zone; B, West-Asturian-Leonese zone (and its southern extension in the Iberian Cordillera); C, Central-Iberian zone; D, Ossa-Morena zone; E, South-Portuguese zone. Fossil localities: 1, 'Sueve'; 2, Fombuena-Herrera (FB, LU, HERR); 3, Calamocha (PO); 4, Aragoncillo (CR, PS); 5, El Pobo (PD); 6, Geo de Albarracín (GA); 7, Truchas (TR); 8, El Atazar (AT); 9, La Bastida (LB); 10, Alia-Navalpino (PSV, HM, RA); 11, Navas de Estena-Retuerta (NE, RE); 12, Ventas (VPA); 13, Benazaire-Puebla de Don Rodrigo (Hd, PR, PI); 14, Herrera del Duque (HD); 15, Pozuelos-Corral de Calatrava (PZ, CO); 16, Sierra de San Pedro (SVA, PC); 17, Santa Eufemia (SEU); 18, Almadén (AC, AM, CHI, GS); 19, Fuencaliente (FU); 20, Calzada-Viso del Marqués (CC, VM); 21, Sierra Morena oriental (ALAM); 22, Cazalla de la Sierra (CS).

formations as summarized and correlated by Hammann *et al.* (1982) and Gutiérrez-Marco *et al.* (1984a, in press).

Most of the bivalves are preserved as internal/external moulds in shales, silty nodules and the sandstones; rare casts of specimens with conjoined valves replaced by hematitic or silty materials have seldom been found.

Text-figure 2 shows the stratigraphic distribution of the species based on accompanying fossils of biostratigraphical value (graptolites, trilobites, brachiopods and microfossils). Nevertheless, it has been shown elsewhere that there is difficulty in correlating the Spanish Ordovician with the British

	LLANVIRN		LLANDEILO	
	Lower	Upper	Lower	Upper
1 <i>Ctenodonta cf. escosurae</i> (SHARPE)	—			
2 <i>Praenucula costae</i> (SHARPE)				
3 <i>Praenucula sharpei</i> n.sp.			-----	
4 <i>Cardiolaria beirensis</i> (SHARPE)		-----		
5 <i>Ekaterodonta hesperica</i> n.sp.	—			
6 <i>Myoplusia bilunata perdentata</i> (BARRANDE)		-----		
7 <i>Cadomia britannica</i> (BABIN)		—		
8 <i>Goniophora (Cosmogoniophora)</i> sp.	—			
9 <i>Modiolopsis? elegantulus</i> SHARPE		-----		
10 <i>Cyrtodontula</i> sp.		—		
11 <i>Glyptarca? lusitanica</i> (SHARPE)				
12 <i>Ananterodonta oretanica</i> BABIN & GUTIÉRREZ-MARCO	—			
13 <i>Babinka prima</i> BARRANDE	—			
14 <i>Coxiconcha britannica</i> (ROUAULT)			-----	
15 <i>Redonia deshayesi</i> ROUAULT				-----
16 <i>Dulcineaia manchega</i> n.gen., n.sp.		-----	-----	

TEXT-FIG. 2. Stratigraphic distribution of Spanish Middle Ordovician bivalve species.

stratotypes of the Llandeilo Series. For this reason, some authors adopt the Bohemian Dobrotivá Series (Havlíček and Marek 1973), with which the Ordovician sequences of the Southern Gondwanan platform ('Mediterranean area') are also easier to correlate. The Dobrotivá Epoch is, however, a possible equivalent of the global standard Teretiusculus Zone. Thus, with reservation, we use the Llandeilo Series in spite of controversy (Whittington *et al.* 1984).

SYSTEMATIC PALAEOLOGY

The classification used by Pojeta (1987) is adopted here. The morphological indexes used in some descriptions are those defined by Babin (1966, p. 28). If not otherwise cited, figured and described specimens are in the Department of Palaeontology, Complutense University of Madrid, Spain. Complementary material is housed in the Laboratory of Palaeontology, University of Brest (LPB), in the Université Claude Bernard – Lyon I (FSL), in the British Museum of Natural History, London (BMNH) and in the Národní Museum of Prague.

Class BIVALVIA Linnaeus, 1758
 Subclass PALAEO-TAXODONTA Korobkov, 1954
 Order NUCULOIDEA Dall, 1889
 Superfamily CTENODONTACEA Wöhrmann, 1893
 Family CTENODONTIDAE Wöhrmann, 1893
 Genus CTENODONTA Salter, 1852

Type species. *Tellinomya nasuta* Hall, 1847, by subsequent designation of Salter (1859, p. 34).

Diagnosis. Nuculaniform ctenodontids lacking prominent concentric ornament.

cf. *Ctenodonta escosurae* (Sharpe, 1853)

Plate 1, figs 1–4

cf. 1853 *Leda escosurae* Sharpe, p. 151, pl. 9, fig. 8.

Material. Two internal moulds (one right valve and one left valve), CR II 2161/OR.

Locality and stratigraphical range. Basal shales of La Venta Formation, Aragoncillo Massif (Iberian Cordillera, Castilian Branch); lowermost Llanvirn.

Description and discussion. Small shell (respectively 13 and 10.5 mm long) with a weak beak situated at the anterior third. Anterior margin and ventral side convex; maximum height located exactly behind the umbo. Posterior end gently elongate and rounded; a very faint depression on the posterior part of the shell produces a discrete inflexion of the ventral margin between the posterior fourth and fifth parts. Characters of the hinge plate unknown. Anterior adductor muscle scar posteriorly fringed by a small high and broad septum. Posterior adductor scar poorly visible and anteriorly limited by a weak undulation of the valve.

Sharpe's material of *Leda escosurae* is BMNH Pl. 4106 (internal mould of a bivalve specimen, figured by Sharpe, pl. 9, fig. 8, which must be considered as lectotype; figured here, Pl. 1, figs 1 and 2) and BMNH Pl. 4138 (internal mould of a right valve, paralectotype).

Sharpe's types are nuculaniform with their elongate posterior end, but the dentition, with numerous chevron-shaped teeth, has no resilifer. Thus these forms must be referred to *Ctenodonta* as used since McAlester (1968) and Pojeta (1971) for *Nuculoida* without a resilifer and with a rostrate end. Our specimens have an outline similar enough to that of *Ctenodonta escosurae*, but their dentition is not preserved and we must leave them in open nomenclature. Barrande (1881, pls 269 and 270) figured several 'species' of '*Leda*' from the Ordovician of Bohemia, but they belong to other genera and are different from *C. escosurae* (Pfab 1934). There are many elongate shells in the Ordovician, and they probably belong to different families or even different orders (e.g. *Thoralia* Morris, 1980 = *Miquelana* Babin, 1982, junior synonym from the Arenig of the Montagne Noire); unfortunately, the material is often poorly preserved.

Superfamily NUCULACEA Gray, 1824
Family PRAENUCULIDAE Pfab, 1934

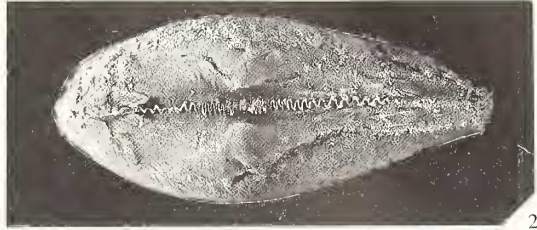
Remarks. Since the revision by McAlester (1968) of the type material, efforts have been made to homogenize the generic designations of palaeotaxodontids from the Lower Palaeozoic. However, some confusion persists because these small bivalves are numerous, variable, sometimes polymorphous and are often badly preserved or distorted. Among the praenuculids, Tunnicliff (1982) has discussed the difficult distinctions between *Praenucula*, *Praeleda*, and *Deceptrix*. We shall try to apply this author's criteria to distinguish *Praenucula* (anterior and posterior teeth subsimilar in size and number; umbo lying in the posterior half) and *Deceptrix* (= *Praeleda*) (posterior teeth smaller and more numerous than the anterior; umbo lying in the anterior half; adductor muscle scars larger and more ventral than in *Praenucula*.)

Genus PRAENUCULA Pfab, 1934

Type species. *Praenucula dispar expansa* Pfab, 1934 (from the Sarka Formation, Llanvirn of Bohemia) by original designation of Pfab, 1934 (pp. 234–235). See discussion under Praenuculidae above.

EXPLANATION OF PLATE I

- Figs 1 and 2. *Ctenodonta escosurae* (Sharpe, 1853). Lectotype (BMNH, Pl. 4106), Middle Ordovician, Portela de Loreda, Serra de Bussaco (Portugal). 1, right view, 2, cardinal view. Both $\times 4$.
- Figs 3 and 4, cf. *Ctenodonta escosurae*. Aragoncillo Massif (Iberian Cordillera), basal part of La Venta Formation, lowermost Llanvirn. 3, internal mould of a right valve (CR-II 2 161/OR), $\times 4$. 4, internal mould of a left valve (CR-II 2 161/OR), $\times 4$.
- Figs 5–9. *Praenucula costae* (Sharpe, 1853). 5–8, Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; 5, internal mould of a right valve showing numerous borings on the ventral part (CC-I 2 169/OR), $\times 4$; 6, detail of the postero-umbonal part of an internal mould of a right valve, the muscle scars (posterior adductor and pedal accessory) show growth lines; some borings are present (CC-I 2 166/OR), $\times 8$; 7, internal mould of a left valve (CC-I 2 168^{bis}/OR), $\times 4$. 8, latex replica of the same, $\times 4$. 9, Ventas con Peñas Aguilera (Toledo), lower part of the Navas de Estena Shales, Lower Llanvirn; internal mould of the continuous dentition of the right valve of a young specimen (VPA 2 171/OR), $\times 8$.



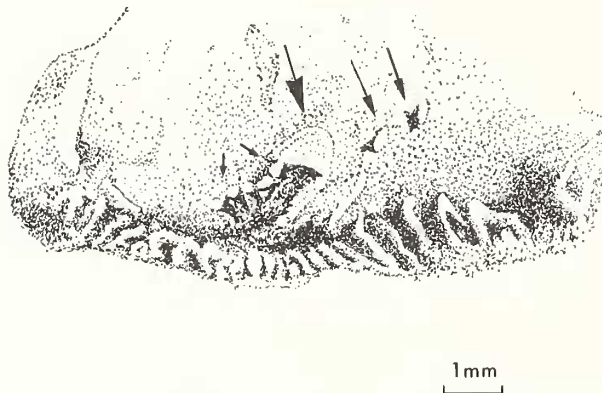
Praenucula costae (Sharpe, 1853)

Plate 1, figs 5-9

1853 *Nucula costae* Sharpe, p. 149, pl. 9, fig. 4.1970 *Praeleda costae* (Sharpe), Bradshaw, p. 630, text-figs 7-10 (synonymy).*Material.* About 320 internal moulds.

Localities and stratigraphical range. Lower Llanvirn to Upper Llandeilo (muddy and sandy facies) of the Cantabrian zone (Sueve), West Asturian-leonese zone (TR-III), Iberian Cordillera (FB-IV, GA-II, HERR-I, PD-I, PO-I), and 34 localities in the Central-Iberian zone (AC-II, ALAM-III, Albadalejo, CC-I & II, CHI-IV, CO-XII and XIV-XVI, HD-IV-VI, HM-II and IV, La Carcel, La Vibora, NE-IV & VII, PI-IV, PR-IX, PSV-III-V, PZ-III, RA-I, IA, II, IVB and VI, SEU-II, SP-IV, VM-I, VPA). This species is particularly common in RA-I, CC-I, VPA, PSV-III/IV and La Vibora.

Description. Shell small, convex, with a strong umbo lying in the posterior half and prominent convex cardinal margin. Ventral margin also convex, the posterior side more or less rounded and the anterior side truncate. In juvenile forms the adductor scars are poorly impressed, but in adults they are more marked. Anterior adductor scar large, oval, parallel with the anterior margin and strongly impressed on its posterior side. Posterior scar smaller and round. Two pedal accessory scars always present; one adjacent to the anterior adductor scar on its dorsal side; the other is elongate and situated half-way along the posterior hinge plate. One specimen (CC 2166/OC) shows growth lines on this scar and on the posterior adductor scar (Pl. I, fig. 6). Specimen RA-I 2167/OR has other scars near the extremity of the umbo (Text-fig. 3).



TEXT-FIG. 3. *Praenucula costae* (Sharpe, 1853). Umbonal view of an internal mould of a left valve (RA-I 2167/OR) showing accessory muscle scars: two small anterior scars (medium arrows), one umbonal scar (large arrow) and four very small posterior scars (between the fine arrows).

The dentition comprises a varying number of teeth according to the size of the shell. The two series, anterior and posterior, are arranged without disruption beneath the umbo (Pl. 1, fig. 8) and so the teeth are difficult to count.

Length of shell (mm) 3, 3.5, 6.5, 7.5, 7.8, 8.5, 10, 10, 10.5, 12, 12.5, 13, 13.5, 14, 15, 16, 16, 17, 19

Number of posterior teeth 6, 7, 6, 9, 6, 10, 8, 13, 10, 15, 14, 14, 11, 13, 14, 16, 21, 15, 17

Number of anterior teeth 6, 5, 6, 9, 6, 7, 7, 11, 9, 10, 12, 10, 9, 13, 13, 12, 10, 12, 13

Several specimens have more numerous posterior teeth, a character also indicated by Bradshaw, and considered by Tunnicliff as a criterion for the genus *Deceptrix*. However, the umbo is in the posterior half, a character of *Praenucula*.

The anterior teeth are convex, beneath the umbo they are orthomorph, and on the posterior hinge plate they are convexo-concave and concave. A single specimen (RA-I 2167/OR) shows an inconspicuous disruption between the two series.

Discussion. Bradshaw (1970) studied, using material from the Armorican Ordovician, the discrimination of the two Sharpe species, *costae* and *ciae*. *P. costae* shows 'two series of teeth arranged at an angle to each other', also figured by Babin (1966, figs 27 and 28; pl. 2, figs 6, 12, 13) under the designation *Palaoneilo ctenodontoides* (this generic conception of *Palaoneilo*, that of Douvillé [1912, p. 38], became outmoded after McAlester's revision in 1968). One of us (C.B.) observed that Sharpe's type of *P. costae* (BMNH, Pl. 4100) shows this disruption. It is only seen in one Spanish specimen (see above); nevertheless the distribution of the teeth, i.e. more numerous in the posterior hinge plate, is close to *P. costae*. Moreover, Bradshaw (1970) wrote "*P. costae* is particularly interesting as it is the more variable of the two species and sometimes exhibits a dental plate similar to that of *P. ciae*". She also figured (text-fig. 10) an internal mould of *P. costae* without the discordance between the two series of teeth.

Another character used by Bradshaw to distinguish between the two species is the pattern of the accessory muscle scars. The umbonal scars are usually preserved and well marked in the Armorican material (Babin 1966, fig. 26; Bradshaw 1970, figs 8, 9, 12), but they are not present or preserved in the Spanish material. On the other hand, the position of the accessory scar lying half-way along the posterior part of the hinge plate is always seen, which, according to Bradshaw, is a feature of *P. costae*. So it seems justified to consider *P. costae* as a polymorphic species and to place the Spanish specimens within it. The variations affecting the dentition and the accessory scars are thus considered dependent on intraspecific variability between geographically isolated populations.

There are other related species of *P. costae* and *P. ciae*; for example, '*Ctenodonta*' *nuda* from the Swedish Middle Ordovician (Soot-Ryen and Soot-Ryen 1960, pl. 1, fig. 1) has a narrower posterior end. It is possible that some of the specimens from Bohemia, illustrated by Barrande (1881, pl 269) as *Leda bohémica*, are closely allied to, if not conspecific with, *P. costae* (Pfab 1934, p. 223, excluded from *C. bohémica* several of Barrande's specimens). Tunnicliff (1982, p. 50) has also compared *P. praetermissa* from the Irish Ashgill with *P. costae* and *P. ciae*. Thus, this palaeotaxodontid morphology was very frequent during the Middle and Upper Ordovician.

Praenucula sharpei n. sp.

Plate 2, figs 1–6

1984b *Deceptrix* n. sp. Martin in Gutiérrez-Marco *et al.*, p. 302.

Holotype. Internal mould of a right valve showing the dentition. RA-I 2148/OR.

Type locality and horizon. 7500 m ESE from Horcajo de los Montes (Ciudad Real), in the El Calvario hillock peak (646 m), N of Los Rasos de Navalaceite hamlet. Reddish shales with coquinas from the upper half of the Navatrasiera Shales; early Upper Llanvirn (*Cacemia* beds).

Derivation of name. Dedicated to Daniel Sharp who was the first describer of Ordovician bivalves from the Iberian peninsula.

Paratypes. RA-I 2 146/OR, 2 147/OR, 2 149/OR, 2 183/OR; NE-IV 2 189/OR (two specimens); PZ-III 2 187/OR, 2 188/OR (two specimens); RE-IX 2 186/OR; SP-IV 2 184/OR; VPA-2 144/OR, 2 145/OR, 2 185/OR (ten specimens).

Diagnosis. Small species of *Praenucula*, convex and high, with few teeth distributed almost equally between the two parts of the hinge plate. Adductor muscle scars not very extended and badly impressed.

Description and discussion. Shells are generally small (of 32 measured specimens, the mean length is 8.6 mm, the range 4.7–15.5 mm). Anterior region is a little elongated and the posterior one rounded. The umbones lie in the posterior half but near the middle of the length (mean of the umbonal index: 56.04). Shell is high (mean of the lengthening index [C. Babin, 1966]: 75.57). The cardinal side is gently arched. Adductor scars discrete, oval, situated in the anterior and posterior angles; a small pedal posterior scar occurs between the posterior adductor and the hinge plate, and an anterior scar adjacent to the upper point of the anterior adductor muscle.

Dentition usually limited to the middle part of the cardinal line with few teeth (generally about 12, ranging from 7 for a shell 5 mm long to 28 for a shell 15.5 mm long). The teeth are nearly similar in size (the posterior ones are a little smaller in the largest specimens).

This species differs from all those described in the literature in its shape and short dentition, and is known only from Spain.

Genus *CARDIOLARIA* Munier-Chalmas, 1876

Type species. By original designation, *Cardiolaria barrandei* Munier-Chalmas, 1876, p. 107, from the Upper Ordovician of the Armorican Massif.

From the specimens of the type-species he could examine, McAlester wrote (1968) 'the dentition immediately below the umbo is not preserved'. One of us (C.B.) has found in the collections of the University of Lille some specimens from the type-locality (la Bouëxière) and one of them shows an edentulous space beneath the umbo, between the two series of teeth. This shows it to be attributable to the genus *Cardiolaria*.

Cardiolaria beirensis (Sharpe, 1853)

Plate 3, figs 4–7

- 1853 *Nucula beirensis* Sharpe, p. 150, pl. 9, figs 11 and 12.
 1918 *Nucula beirensis* Sharpe, Born, p. 337.
 1970 *Cardiolaria beirensis* (Sharpe), Bradshaw, p. 624, figs 1–4 (see for synonymy).
 1978 *Cardiolaria beirensis* (Sharpe), Pojeta, pl. 2, fig. 15.

Material. About 180 internal moulds. The species is common from FB-IV, NE-VII, RA-I, RE-VI and La Vibora.

Localities and stratigraphical range. Late Lower Llanvirn-Upper Llandeilo, relatively scarce in shales but well represented in sandstone facies. The studied samples come from the West Asturian-leonese zone (loc. TR-III, Iberian Cordillera (FB-IV, GA-II) and the Central-Iberian zone (ALAM-IV, CHI-IV-V, CO-XII and XIII A, FU-IX, HD-IV and VI, La Carcel, La Vibora, NE-VII, PI-III and IV, PSV-III and V, RA-I, RE-VI, SVA-II).

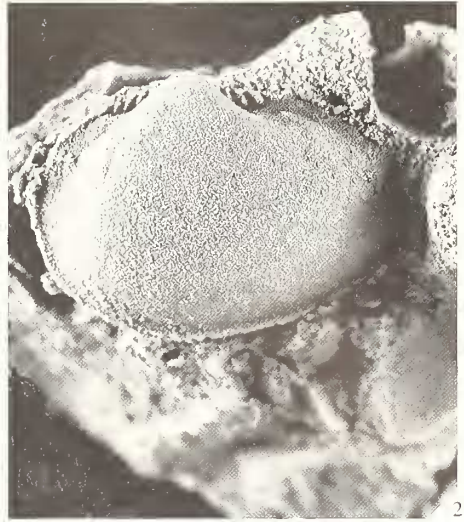
Description and discussion. Shell outline rounded and moderately convex, on the internal moulds with a strong prosogyrous beak. Anterior adductor muscle scar fringed on its internal margin by a strong myophoric buttress; posterior adductor scar little impressed (the accessory scars are not visible except for an anterior pedal scar adjacent to the anterior adductor scar). Dentition comprising five or six anterior teeth and 15 to 20 small posterior teeth. The two series are discordant and separated by an edentulous space below the umbo (Pl. 3, figs 4 and 5) though Bradshaw (1970) noted that juvenile specimens have a continuous dentition. We have observed two very young specimens (FSL 550 094 and FSL 550 095) in the Armorican material with a length of 2 mm and 4.2 mm respectively; their weak adductor scars and dentition are interesting ontogenetically (Text-fig. 4).

It is undoubtedly material of this species from Almadén that de Verneuil and Barrande (1856) determined as *Nucula hopensacki*. Douvillé (1912, p. 439) drew the hinge area, with a wrong age attribution to the Cambrian; his original material appears to have been lost.

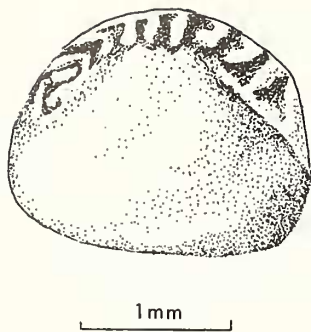
We also consider that four small specimens (Pl. 3, fig. 6, 7) from locality RA-I 2 179/OR to RA-I 2 181/OR are possible juvenile forms of *C. beirensis*. Their lengths are 6.5 mm, 6.5 mm, 9 mm, and 10.5 mm. The hinges exhibit a continuous series of 22 to 25 posterior and umbonal teeth (these latter very small) and four or five

EXPLANATION OF PLATE 2

Figs 1–6. *Praenucula sharpei* n. sp. 1, right view of an internal bivalve mould (VPA 2 144/OR), Ventas con Peña Aguilera (Toledo), lower part of the Navas de Estena Shales, Lower Llanvirn, $\times 5$. 2 and 3, paratypes, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 2, internal mould of a right valve (RA-I 2 146/OR), $\times 8$; 3, internal mould of a left valve (RA-I 2 149/OR), $\times 8$. 4, internal mould of a left valve from San Pablo de los Montes (Toledo), Lower Llanvirn (SP-IV 2 184/OR), $\times 8$. 5, holotype, same locality as paratypes, internal mould of a right valve (RA-I 2 148/OR), $\times 8$. 6, internal mould of a left valve from Venta con Peña Aguilera (Toledo), Lower Llanvirn, $\times 5$.



BABIN and GUTIÉRREZ-MARCO, *Praenucula sharpei* n.sp.



TEXT-FIG. 4. *Cardiolaria beirensis* (Sharpe, 1853). Internal mould of the right valve of very young specimen (FSL 550 094) from the Armorican Massif. The beak is broken and the dentition appears continuous.

anterior teeth which are stronger. A very similar arrangement was figured by Bradshaw (1970, fig. 1). However, the Spanish specimens have peculiar muscular impressions. The adductor scars are well developed and there is a strong anterior myophoric plate, but the accessory muscle scars are deeply impressed and numerous. There is a prominent anterior pedal scar adjacent to the posterior adductor; these pedal scars are elongated perpendicular to the cardinal margin. There are three other accessory scars, with one on the posterior slope of the umbonal region and the others in the median region of the valve (Pl. 3, fig. 6, 7). These specimens were determined as *Tancrediopsis ezquerrae* (Sharpe) by Gutiérrez-Marco *et al.* (1984*b*), but they do not have the adductor scars of that species which also possesses larger and fewer posterior teeth. We also note that *T. ezquerrae*, described from Portugal and common in the Armorican Massif, is absent from the observed Spanish material (another bad specimen [RE-VI 2 214/OR] may belong to the genus *Tancrediopsis* but not to the species *T. ezquerrae*). In these small specimens of *C. beirensis* the partition beneath the umbo of the two series of teeth appears late during ontogeny with later resorption; see also Bradshaw (1970). In some forms, the accessory musculature is reduced during ontogeny.

Family TIRONUCULIDAE Babin, 1982

Genus EKATERODONTA Babin, 1982

Type species. By original designation, *Ekaterodonta courtessolei* Babin, 1982, p. 38, from the Arenig of the Montagne Noire (South of France).

Ekaterodonta hesperica n. sp.

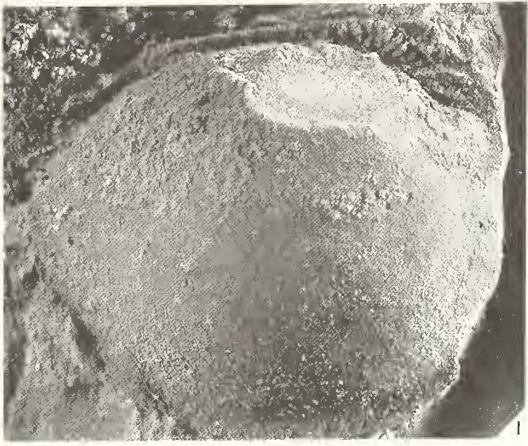
Plate 3, figs 1–3

Holotype. Internal mould of a right valve showing the dentition, CR-II 2 152/OR.

EXPLANATION OF PLATE 3

Figs 1–3. *Ekaterodonta hesperica* n. sp. Aragoncillo Massif (Iberian Cordillera), basal part of La Venta Formation, lowermost Llanvirn. 1, holotype, internal mould of a right valve showing the dentition (CR-II 2 152/OR), $\times 10$. 2, paratype, internal mould of a left valve (CR-II 2 154/OR), $\times 6$. 3, paratype, internal mould of a right valve (CR-II 2 153/OR), $\times 6$.

Figs 4–7. *Cardiolaria beirensis* (Sharpe, 1853); 4 and 5, La Vibora, ? Upper Llandeilo, latex replica of two right valves showing the discordant series of teeth (FSL 550 109, FSL 550 110, $\times 6$. 6 and 7, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 6, internal mould of a left valve showing accessory muscle scars (RA-I 2 179/OR), $\times 8.5$; 7, internal mould of a right valve with accessory scars (RA-I 2 181/OR), $\times 10$.



Type locality and horizon. 2300 m N of Aragoncillo village, and 900 m WNW of Aragoncillo mountain (1518 m), in the talus of the first track to the Canaleja spring. Dark shales of the basal part of La Venta Formation; earliest Lower Llanvirn.

Derivation of name. After the Hesperian Massif, where most of the Ordovician outcrops in the Iberian Peninsula are situated.

Paratypes. Internal moulds CR-II 2 153/OR, CR-II 2 154/OR, CR-II 2 155/OR and CR-II 2 156/OR (6 specimens).

Diagnosis. Shell small, rounded and smooth, with anterior beak; anterior adductor muscle scar small, rounded, faintly impressed; posterior one is indistinct; dentition has two short anterior pseudolateral teeth, some small orthomorphic teeth beneath the umbo and, on the posterior hinge plate, some small chevron-shaped teeth and a large lamellar tooth.

Description and discussion. The shell is small (length range from 6.5 to 11 mm) and high (average lengthening index 84.80 based on 9 specimens); beak is curved and anterior (average umbonal index 26.57); outline rounded anteriorly and ventrally with a slightly truncate posterior end. The dentition is only complete on the holotype; its poor preservation and fragility do not allow a cast to be made. It comprises two short lamellar anterior teeth perpendicular to the anterior margin of the hinge plate and a posterior pseudolateral tooth; the latter possibly corresponds to the extension of the upper arm of an underumbonal tooth and surmounts the 8 or 9 more posterior teeth of the series.

The outline, its ornamentation and particularly its dentition, are very similar to the type species. Nevertheless, this species differs in its weak adductor muscle scars.

Superfamily NUCULANACEA Adams and Adams, 1858

Family MALLETIIDAE Adams and Adams, 1858

Genus MYOPLUSIA Neumayr, 1884

Type species. *Leda bilunata* Barrande, 1881, by subsequent designation of McAlester, 1968, p. 35.

Myoplusia bilunata perdentata (Barrande, 1881)

Plate 4, fig. 1-8

- 1881 *Leda bilunata* Barrande, pl. 270, I, figs 13-24.
 1881 *Leda perdentata* Barrande, pl. 270, II, figs 1-9.
 pars 1918 *Leda bohémica* Barrande, Born, p. 338, pl. 24, fig. 5.
 1934 *Ctenodonta bilunata perdentata* (Barrande), Pfab, p. 227, pl. 2, figs 12-13.

EXPLANATION OF PLATE 4

Figs 1-7. *Myoplusia bilunata perdentata* (Barrande, 1881) 1, many internal moulds of valves of *Myoplusia* from Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo, $\times 2.7$. 2 and 3, Barrande's specimen (1881, pl. 270, figs 1-4), paratype after McAlester, 1968, Sterboholý (Czechoslovakia), Middle Ordovician, Národní Museum Collections (Prague), left and cardinal views of an internal bivalve mould (phot. J. Kříž), $\times 7$. 4, Barrande's specimen (1881, pl. 270, I, fig. 21-24), cardinal view of a partial bivalve mould (phot. J. Kříž), $\times 7$. 5-7, Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; 5, internal mould of a right valve (CC-I 2 131/OR), $\times 7$; 6, latex replica of the dentition of a left valve (CC-I 2 129/OR), $\times 10$; 7, latex replica of a right valve (CC-I 2 176/OR), $\times 7$. 8, Barrande's specimen (1881, pl. 270, II, fig. 7-9), also figured by Pfab (1934, pl. II, fig. 13), Sterboholý (Czechoslovakia), Middle Ordovician Národní Museum Collections (Prague), internal mould of a right valve (phot. J. Kříž), $\times 5$.



- ?1939 *Ctenodonta* (*C.*) *bilunata perdentata* Pfab [sic], Maillicux, p. 33, pl. 2, figs 19–22.
 1966 *Ctenodonta* sp., Babin, p. 299, pl. 1, fig. 8.
 1972 *Myoplusia* cf. *bilunata perdentata* (Barrande), Babin and Mélou, p. 85, pl. 7, figs 1 and 2.
 1973 *Myoplusia* cf. *bilunata perdentata* (Barrande), Babin and Robardet, p. 31, pl. 2, figs 1–6.

Material. Seventy-nine internal and some external moulds.

Localities and stratigraphical range. Upper Llanvirn-Upper Llandeilo (Spanish record of the species); muddy and sandy facies from the Iberian Cordillera (GA-II) and the Central-Iberian zone (ALAM-III, Albadalejo, CC-I, PSV-IV, PZ-III, RA-I, RA-IV, RE-VII).

Description and discussion. Shell always small, length less than 10 mm (average for the Spanish material 6.9 mm). Cardinal margin convex, anterior side weakly truncate; pallial edge widely convex in anterior part (greatest height below the beak), then there is a faint inflexion and the elongate posterior end is less high than the anterior one. Beak prosogyrous, situated towards the anterior third of cardinal line, on internal moulds acute and bent. Adductor muscle scars strongly impressed. Anterior scar oval, perpendicular to cardinal plate; posterior one with anterior linear side inclined almost to the hinge line, and a rounded posterior side. The accessory scars comprise a scar occurring above the posterior adductor.

Dentition paleotaxodont, number of teeth variable (16–30) according to size of the shell. Anterior teeth slightly convex; teeth beneath umbo thin and orthomorph; some concavo-convex teeth follow them without discontinuity from the concave posterior teeth.

Pfab (1934) reduced the contemporaneous species of Barrande (*bilunata* and *perdentata*) to the rank of varieties of the single species *bilunata*. The Spanish specimens belong, without doubt, to the species *bilunata* but it is difficult to assign them to either subspecies. They have the anterior end slightly truncated as in *bilunata bilunata* and the umbonal scars also point to this subspecies. But the narrower posterior end suggests *bilunata perdentata*, which also sometimes has the faintly sinuous pallial margin of the Spanish specimens (we are indebted to Dr J. Kříž for photographs of the specimen figured by Barrande 1881, pl. 270, I, figs 7–9 and by Pfab 1934, pl. 2, fig. 13, showing this morphology; see Pl. 4, fig. 8). Finally, the hinge with the particularly concave posterior teeth is similar to the type figured by Pfab (pl. I, fig. 5a) as *M. bilunata perdentata*. We therefore refer our material to *M. bilunata perdentata*. To exclude it would create another geographic subspecies with some characters of each Bohemian subspecies. Direct comparison with the Armorican material shows that they are very similar, with but tiny differences such as in the position of the posterior adductor muscle scar.

Genus CADOMIA Tromelin, 1877

Type species. By monotypy *Cadomia typa* Tromelin, 1877, p. 48; fig in Bigot, 1890, pl. 23, fig. 3.

Cadomia britannica (Babin, 1966)

Plate 5, fig. 2

- 1966 *Ctenodonta britannica* Babin, p. 54, pl. 1, fig. 1
 1984b *Deceptrix* ? *britannica* (Babin), Gutiérrez-Marco *et al.*, p. 302.

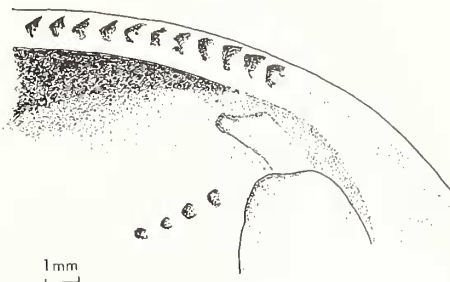
Material. Ten external moulds of right and left valves.

Localities and stratigraphical range. This rare species is known only from six localities in the southern part of the Central-Iberian zone (CHI-IV, Fontanosas, HD-VI, NE-VII, PI-III and SEU-II); muddy facies close to the Llanvirn-Llandeilo boundary.

Description and discussion. All the valves are large (length, 30–40 mm); the outline is oval with the beak in the anterior third of the shell. Dentition with a continuous series of teeth; 6–8 anterior teeth convex, 6–7 teeth beneath the umbo orthomorph, 25–30 posterior teeth convex. Adductor muscle scars clearly marked, oval, but not very large; accessory scars with a pedal anterior one, situated behind the dorsal extremity of the anterior adductor, and a pedal posterior one in contact with the dorsal margin of the posterior adductor. Another pronounced scar near the hinge plate, half-way between the posterior adductor and the umbo. Several small

scars situated on the anterior side of the umbonal cavity; lastly, four tiny scars (?) seem to precede the posterior adductor (Text-fig. 5). The Spanish specimens are identical with those from the Armorican Massif (Babin 1966). Generic attribution is difficult; we tentatively assign this species to *Cadomia* because it is an inequilateral shell with numerous taxodont teeth without disruption beneath the umbo. This species is not very common and seems to be restricted to the basal Llandeilo.

TEXT-FIG. 5. *Cadomia britannica* (Babin, 1966). Upper posterior region of a latex replica (CH-I-V 2 143/OR) showing four minute muscle scars in front of the posterior adductor.



Subclass ISOFILIBRANCHIA Iredale, 1939
 Order MODIOMORPHOIDA Newell, 1969
 Superfamily MODIOMORPHACEA Miller, 1877
 Family MODIOMORPHIDAE Miller, 1877
 Genus GONIOPHORA Phillips, 1848
 Subgenus COSMOGONIOPHORA McLearn, 1918

Type species. *Goniophora bellula* Billings, 1874.

Goniophora (*Cosmogoniophora*) sp.

Plate 5, figs 3 and 4

Material. Twenty-five internal and some external moulds of right and left valves.

Locality and stratigraphical range. Recorded only from the basal beds of the La Venta Formation, locality CR-II in the Iberian Cordillera; earliest Lower Llanvirn.

Description and discussion. Small shell (the length of the complete specimens varies from 13 to 22 mm), moderately convex, with a weak umbo and the typical outline of *Goniophora*, i.e. with an elongate postero-ventral angle into which leads a strong carina proceeding from the beak. Ornamentation of fine concentric striae in front of the carina, but of radial costae on the slope behind the carina. Hinge unknown. No muscle scar observable. With its radial costae, this form can be assigned to the subgenus *Cosmogoniophora* but no specific name can be proposed. The genus is known from the Lower Ordovician to the Devonian.

Genus MODIOLOPSIS Hall, 1847

Type species. *Pterinea modiolaris* Conrad, 1838.

Modiolopsis? elegantulus Sharpe, 1853

Plate 5, fig. 1

1853 *Modiolopsis elegantulus* Sharpe, p. 152, pl. 9, fig. 15.

Material. Forty-four internal and some external moulds of right and left valves.

Localities and stratigraphical range. Upper Llanvirn to Upper Llandeilo (muddy facies only) from the Iberian Cordillera (HERR-I, LU-II) and the Central-Iberian zone (AM-I, HD-X, PR-IX, PZ-III, RA-I, III and VI B, RE-IX and IX B).

Description and discussion. Inequilateral valves with rectilinear cardinal hinge; beak, situated between the middle and the anterior third and slightly projected. Greatest height just exceeding the cardinal length. This height, extending from the beak to the postero-ventral part, coincides with the greatest convexity of the shell. Anterocardinal angle rounded; posterocardinal angle obtuse (about 130°). Shell very thin and internal moulds showing clearly the ornamentation of concentric undulations. Hinge apparently edentulous with a short ligament groove behind the beak (?). No muscle scar visible.

The material is poor and does not allow straightforward generic attribution. The morphology, the ornamentation and the edentulous hinge can be as easily compared with *Modiolopsis* among the Modiomorphidae as with some Posidoniidae. The species *elegantulus* was described by Sharpe (1853) based on a single specimen from the Ordovician of Portugal and is probably conspecific with the Spanish material.

Subclass PTERIOMORPHIA Beurlen, 1944
Order ARCOIDA Stoliczka, 1871
Superfamily CYRTODONTACEA Ulrich, 1894
Family CYRTODONTIDAE Ulrich, 1890
Genus CYRTODONTULA Tomlin, 1931

Type species. *Whitella obliquata* Ulrich, 1890.

Cyrtodontula sp.

Plate 5, figs 6 and 7

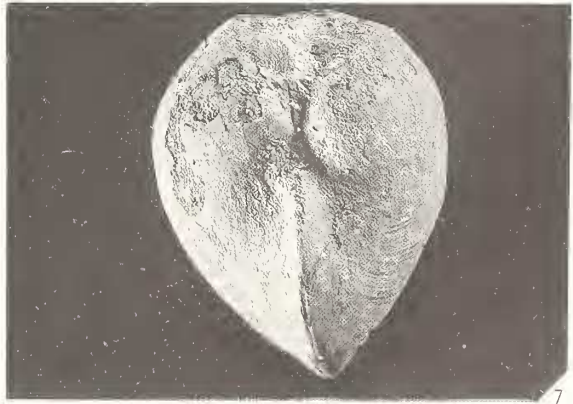
Material. A bivalve mould (CHI-V 2 142/OR) and a partially complete specimen.

Localities and stratigraphical range. Llanvirn-Llandeilo boundary; very rare in the Central-Iberian zone (CHI-V and PI-III)

Description and discussion. The badly preserved specimen is strongly inflated and very inequilateral with beaks near the anterior margin. On this internal mould some preserved fragments of the shell show that a clear ornament is superposed on the concentric striae (Pl. 5, fig. 6). The dorsal margin is partially broken behind the beak but the general morphology is very similar to that of many cyrtodontids (*Cyrtodontula*, *Vanuxemia*) or

EXPLANATION OF PLATE 5

- Fig. 1. *Modiolopsis ? elegantulus* Sharpe, 1853. Pozuelos de Calatrava (Ciudad Real), Valdemorillo Shales, Upper Llandeilo, internal mould of a right valve (PZ-III 2 151/OR), $\times 4$.
Fig. 2. *Cadomia britannica* (Babin, 1966). Chillón (Ciudad Real), upper half of the Rio Shales, early Upper Llanvirn, internal mould of a right valve (CH-I-IV, 2 143/OR), $\times 1.8$.
Figs 3 and 4. *Goniophora (Cosmogoniophora)* sp. Aragoncillo (Guadalajara), basal beds of La Venta Formation, earliest Lower Llanvirn. 3, partial internal mould of a left valve (CR-II 2 163/OR), $\times 3$. 4, internal mould of a right valve (CR-II 2 162/OR), $\times 5$.
Fig. 5. *Babinka prima* Barrande, 1881. Navas de Estena (Ciudad Real), lower third of the Navas de Estena Shales, Lower Llanvirn, internal mould of an elongate specimen (NE-III 2 128/OR), $\times 2$.
Figs 6 and 7. *Cyrtodontula* sp. Chillón (Ciudad Real), upper half of the Rio Shales, Llanvirn/Llandeilo boundary, left and anterior views of an internal bivalve mould (CH-I-IV 2 142/OR), $\times 2$.



some modiomorphids like *Plethocardia*. The absence of data concerning the hinge area makes precise generic attribution difficult. However, the apparent absence of a marked anterior adductor scar indicates tentative inclusion within *Cyrtodontula*. De Verneuil and Barrande (1856, p. 990, pl. 27, fig. 5) erected *Cucullaea caravantesi* for a gibbous shell from the Puebla de Don Rodrigo area which might be the same, in spite of a longer postumbonal cardinal part; however we have not found it in de Verneuil's collections. The morphology of this bivalve suggests an endobysate mode of life as proposed by Frey (1980) for *Vanuxemia*. The genus *Cyrtodontula* is cited from the Upper Ordovician in North America (Richmondian) and in the Baltic area (Isberg 1934), from the Middle Ordovician of Norway (Soot-Ryen and Soot-Ryen 1960), and the 'first records of the genus from the Southern Hemisphere' were given by Pojeta and Gilbert-Tomlinson (1977) from the Arenigian and Trentonian (= late Middle Ordovician?) of Australia.

Subclass HETEROCONCHIA Hertwig, 1895
Order ACTINODONTOIDA Douvillé, 1912
Family CYCLOCONCHIDAE Ulrich, 1894

The diagnosis of the family given by Pojeta and Gilbert-Tomlinson (1977) is 'actinodontids with numerous elongate teeth with lack of denticles'. The species described below, *Glyptarca? lusitanica*, has microcrenulate teeth and its attribution to this family may therefore be debateable. However, the family Lyrodesmatidae with crenulate teeth is characterized, by the same authors, by 'teeth radiating ventrally from immediately below the beak' and is less appropriate. Thus, we consider that *Glyptarca?* can indeed be considered as a member of Cycloconchidae; the diagnosis of the family should therefore be extended to include the possible presence of denticles on the teeth. In the description of the dentition, we use the terminology pseudocardinals and pseudolaterals proposed by Pojeta and Runnegar (1985, p. 320).

Genus GLYPTARCA Hicks, 1873

Type species. *Glyptarca primaeva* Hicks, 1873 by subsequent designation of Carter, 1971, p. 258.

Glyptarca? lusitanica (Sharpe, 1853)

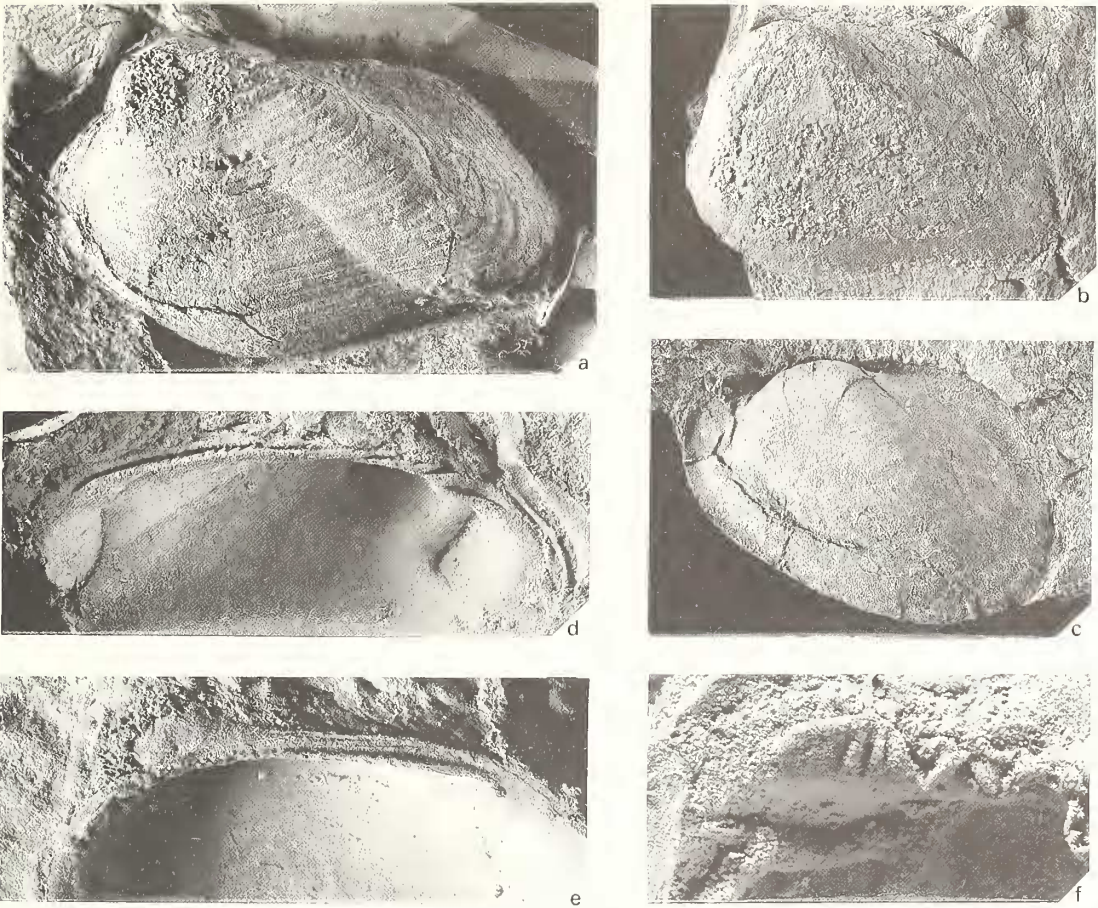
Text-fig. 6

- 1853 *Dolabra? lusitanica* Sharpe, p. 151, pl. 9, fig. 3.
?1853 *Cypricardia? beirensis* Sharpe, p. 152, pl. 9, fig. 16.
1856 *Arca naranjoana* de Verneuil and Barrande, p. 989, pl. 26, fig. 12.
1912 *Actinodonta acuta* Barrois, Douvillé, p. 440, fig. 12 (non Barrois, 1891).
1918 *Modiolopsis? lusitanica* (Sharpe), Born, p. 342.
1966 *Actinodonta naranjoana* (de Verneuil and Barrande) Babin, p. 233, pl. 10, figs 5, 7, 11. See for synonymy; add:
1970 *Actinodonta naranjoana* (de Verneuil and Barrande) Bradshaw, p. 636, text-figs 13–15.
1978 *Glyptarca naranjoana* (de Verneuil and Barrande), Morris, pl. 1, fig. 2.
1984 *Glyptarca naranjoana* (de Verneuil and Barrande), Gutiérrez-Marco *et al.*, p. 302.
1985 *Glyptarca? naranjoana* (de Verneuil and Barrande), Babin & Gutiérrez-Marco, fig. 4.

Material. About 280 specimens. The species is particularly common at VPA, NE-VII, la Vibora, CC-I, RA-I and FB-IV.

Localities and stratigraphical range. Widely distributed in the Llanvirn and Llandeilo shales and sandstones of the Hesperian Massif from the West-Asturian-leonese area (TR-III), Iberian Cordillera (FB-I, FB-IV, LU-II, PO-I) and 38 localities in the Central-Iberian zone (AC-I-III) Albadaledo, CC-I and II, CHI-IV, CO-XII, XIII A, XIV-XVI, FU-IX, HO-IV, LB-I, la Carcel, la Vibora, NE-IV and VII, PI-II-IV and IX, PR-IX, PSU-II-III and V, PZ-III, RA-I, I A and IV B, RE-VI and VII, SEU-II, SP-IV, SVA-II, VM-I, VPA).

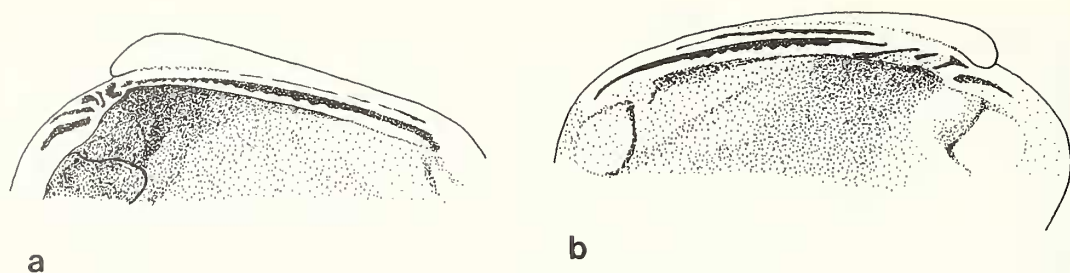
Description and discussion. Shell equivalve, inequilateral, more or less convex; outline slightly variable with subparallel cardinal and ventral margins and a more or less truncate posterior side; ornamentation of fine



TEXT-FIG. 6. *Glyptarca? lusitanica* (Sharpe, 1853). *a, c*. Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; *a*, left view of a latex replica of an external bivalve mould showing the ornamentation (CC-I 2 175/OR), $\times 3$; *c*, internal mould of an atypical left valve (CC-I 2 175/OR), $\times 3$. *b*, Alia (Cáceres), middle part of the Navas de Estena Shales, early Upper Llanvirn; internal mould of a left valve (PSV-III 2 176/OR), $\times 3$. *d*, Corral de Calatrava (Ciudad Real), middle part of the Alisedas Shales, late Lower Llanvirn; latex replica of the dentition of a left valve (CO-XV 2 132/OR), $\times 3.3$. *e*, Calzada de Calatrava (Ciudad Real), Guindo Shales, late Lower Llandeilo; latex replica of a right valve showing the dentition with the two short anterior pseudolateral teeth, the small pseudocardinals, the elongate and microcrenulated posterior pseudolateral (CC-I 2 209/OR and CC-I 2 140/OR), $\times 3.3$. *f*, Retuarta de Bullaque (Ciudad Real), Navas de Estena Shales, Upper Llanvirn; latex replica showing the microcrenulations of an anterior pseudolateral tooth (RE-IV 2 137/OR), $\times 10$.

concentric striae (Text-fig. 6*a*); blunt carina extending from the beak to the posteroventral angle. Two adductor muscle scars variably impressed, large and round. Accessory muscle scars varying. Bradshaw (1970, fig. 13) figured seven scars which are often not visible; on the other hand, we have observed minute scars posteriorly adjacent to the anterior adductor scar, perhaps corresponding, to labial palps muscles.

Dentition very characteristic. Right valve (Text-figs 6*e* and 7*a*; see also Babin and Gutiérrez-Marco 1985, fig. 4), with two short, lamellar anterior pseudolaterals; the more anterior parallel to the hinge place edge, the second oblique; below the beak, two pseudocardinals variably flexed; the latter is overlapped by an elongate posterior pseudolateral with microcrenulations on two-thirds or three-quarters of its length. The anterior tooth of one specimen has peculiar crenulations on its ventral face (Text-fig. 6*f*). Left valve (Text-figs 6*d* and 7*b*)



TEXT-FIG. 7. *Glyptarca ? lusitanica*, diagrams of dentition. *a*, right valve. *b*, left valve.

showing two microcrenulate posterior pseudolaterals which are often strongly marked and which were considered at one stage as taxodont teeth: 'a long posterior plate parallel to the hinge line, which is crossed by numerous small teeth or crenulations' (Sharpe 1853); 'charnière pourvue de petites dents placées en ligne droite' (de Verneuil and Barrande 1856) [our emphasis]. Opisthodontic ligament placed in a fine groove.

This Ordovician material is often distorted or flattened, the morphology of the shell is variable, for example in the accentuation of the carina. Nonetheless, there is no reason to distinguish several species. *Cypricardia ? beirensis* Sharpe (1953) that de Verneuil and Barrande (1956) also distinguished, without a figure, also probably belongs to the same species (some specimens from Sharpe's locality, Ribo de Baixo, suggest this is likely). Delgado (1908) made use of the three designations *Dolabra ? lusitanica*, *Cypricardia ? beirensis*, and *Arca naranjoana* without any figures. Born (1918) pointed out that a form from Bohemia, designated *Modiolopsis veterana* by Barrande (1881, pl. 259, III) has some similarities to the present species.

The species *Arca naranjoana* de Verneuil and Barrande, 1856 (= *Dolabra ? lusitanica* Sharpe, 1853) was tentatively attributed to the genus *Actinodonta* by Babin (1966) and Bradshaw (1970), and later to *Glyptarca* (Morris 1978). In fact, this species differs from *Actinodonta* (and from *Cycloconcha*) which have more numerous teeth with anterior pseudolaterals, radiating more regularly from below the umbo: these genera do not have microcrenulations on the teeth. Morris (1978) employed the generic designation *Davidia* Hicks, 1873 for the Ordovician species *ramsayensis* (Hicks 1873) and *carinata* (Barrois 1891). Nevertheless, Carter (1971) pointed out that the type species *Davidia ornata* Hicks is unusable and placed it tentatively in synonymy with *Actinodonta ramsayensis* whose dentition is poorly known. In the same way, *Actinodonta carinata* Barrois does not provide clear information with regard to the dentition beneath the umbo (Babin 1966). So, the use of *Davidia* would require further investigation. Lastly, *Glyptarca* is a poorly defined genus (Carter 1971) with a small edentulous space between the anterior and posterior teeth (Morris 1978; Pojeta 1985). The Spanish species does not present a similar space in the dentition (Text-fig. 7) and we refer it to *Glyptarca* with a query.

Glyptarca ? lusitanica is very common in the Iberian Peninsula and the Armorican Massif. Morris (1978, pl. 1, fig. 2) has figured a specimen from Shropshire and Fortey and Morris (1982) indicate the presence of *Glyptarca* cf. *naranjoana* from the Hanadir Shales (Llanvirn) in Saudi Arabia.

Genus ANANTERODONTA Babin and Gutiérrez-Marco, 1985

Ananterodonta oretanica Babin and Gutiérrez-Marco, 1985

Text-fig. 9f

This species has recently been described on the basis of a single specimen from the Lower Llanvirn of San Pablo de los Montes (Toledo). Its phylogenetic significance is considered below.

Family BABINKIDAE Horný, 1960

Genus BABINKA Barrande, 1881

Babinka prima Barrande, 1881

Plate 5, fig. 5

Spanish material of this species has recently been revised by Gutiérrez-Marco and Babin (1988); it is only cited and illustrated here. Its geographic distribution is discussed below.

?Family COXICONCHIDAE Babin, 1977

Genus COXICONCHA Babin, 1966

Coxiconcha britannica (Rouault, 1851)

This species was revised by Babin (1977), who proposed a subfamily Coxiconchinae within the Modiomorphidae. According to Pojeta and Runnegar (1985), the family belongs, in the subclass Isofilibranchia, with Babinkidae placed amongst the Heteroconchia. If so, it also seems justified to place *Coxiconcha* here because of its relations with *Babinka*.

C. britannica is very common (584 specimens were collected) in Llanvirn shales and locally also in the early Lower Llandeilo beds. After its disappearance in the muddy facies in younger beds of the Llandeilo, the last record of the species seems to be from the Upper Llandeilo sandy facies (only from ALAM-IV). The studied material comes mainly from 34 localities in the Central-Iberian zone (AC-I, ALAM-III and IV, Albadalejo, CHI-I, IV and V, CO-X, XII and XII A, FU-IX, HD-I, VI and VII, HM-I, IV and V, NE-III-VII, PI-II, III and IX, PS-III, RA-I, I A and I B, RE-II, SEU-II, SP-IV, VM-I, VPA) with only one locality in the West Asturian-leonese zone (TR-III).

Family REDONIIDAE Babin, 1966

Diagnosis. Is here emended to include the new genus *Dulcineaia* (see below). Very inequilateral actinodontoids with anterior and recumbent beaks; a high myophoric buttress limits the anterior adductor muscle posteriorly; hinge plate bearing one or two short pseudocardinal teeth and one or two elongate posterior pseudolaterals; teeth smooth or microcrenulated.

Genus REDONIA Rouault, 1851

Type species. *Redonia deshayesiana* Rouault, 1851, p. 364.

Diagnosis. Redoniidae with smooth teeth and chevron-flexed pseudocardinals.

Remarks. *Redonia* is very common in the southern part of the Gondwanan shelf, and the Spanish material is significant in producing new information leading to its redescription. Unfortunately, the original description (with a misorientation) and illustrations given by Rouault are not very informative and the original material is apparently lost. In the collections of the University of Rennes, there are some very poor specimens, possibly from Rouault's collections but not those figured by him; they come from Gahard (north of Rennes), a locality cited by Rouault, and from Guichen (south of Rennes). From the collections of the Muséum National d'Histoire Naturelle (Paris), we have examined three specimens from localities in Loire-Atlantique (south of the Armorican Massif) none of which is Rouault's material. In the University of Lyon, Verneuil's collections contain specimens from Riadan (south of Rennes) from Vitré (another locality cited by Rouault) and from Brix (Manche). In all these collections, the specimens are labelled *R. deshayesiana* or *R. duvaliana* without discriminating characters. We believe that the descriptions and drawings of Rouault refer to a single species, based on material from Gahard. The present revision requires the designation of a neotype for *R. deshayesi*. The material from the localities near Rennes is badly preserved and its age is not precisely known. Therefore, we select a neotype from the equivalent Postolon nec Formation in the western part of the Armorican Massif (see below).

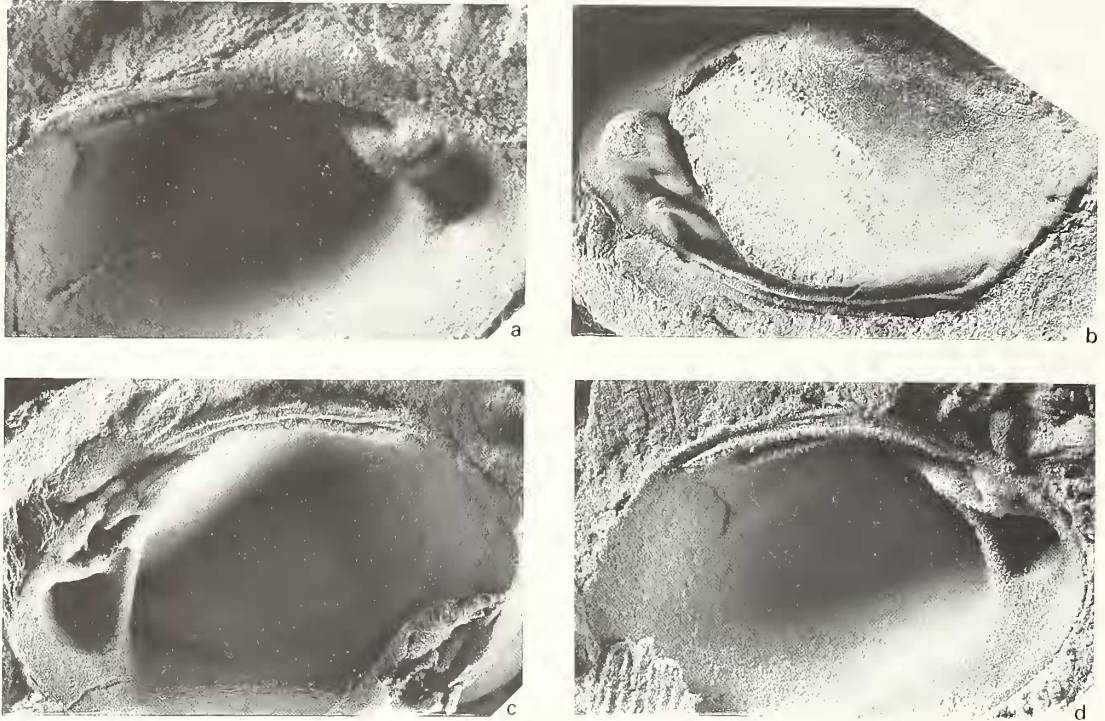
Redonia deshayesi Rouault, 1851

Plate 6, figs 1–7; Text-figs 8 and 9

Synonymy. See Babin 1966, p. 246. Add:

- 1881 *Redonia bohemica* Barrande, pl. 268, figs 1–26.
- 1918 *Redonia deshayesiana* Rouault, Born, p. 339, pl. 25, fig. 1a–f.
- 1918 *Redonia deshayesiana* var. *duvaliana* Rouault, Born, p. 341, pl. 25, figs 2a–f.
- 1950 *Redonia deshayesi* Roemer em. Borneman (sic!), Termier and Termier, pl. 163, fig. 2.
- 1950 *Redonia bohemica* Barrande, Termier and Termier, p. 87, pl. 165, figs 1–3, 6–9.
- 1950 *Redonia megalodontoides* Termier and Termier, p. 87, pl. 165, figs 4 and 5.
- 1951 *Redonia deshayesiana* Rouault em. Born, Gigout, p. 296, pl. 2, fig. 14.

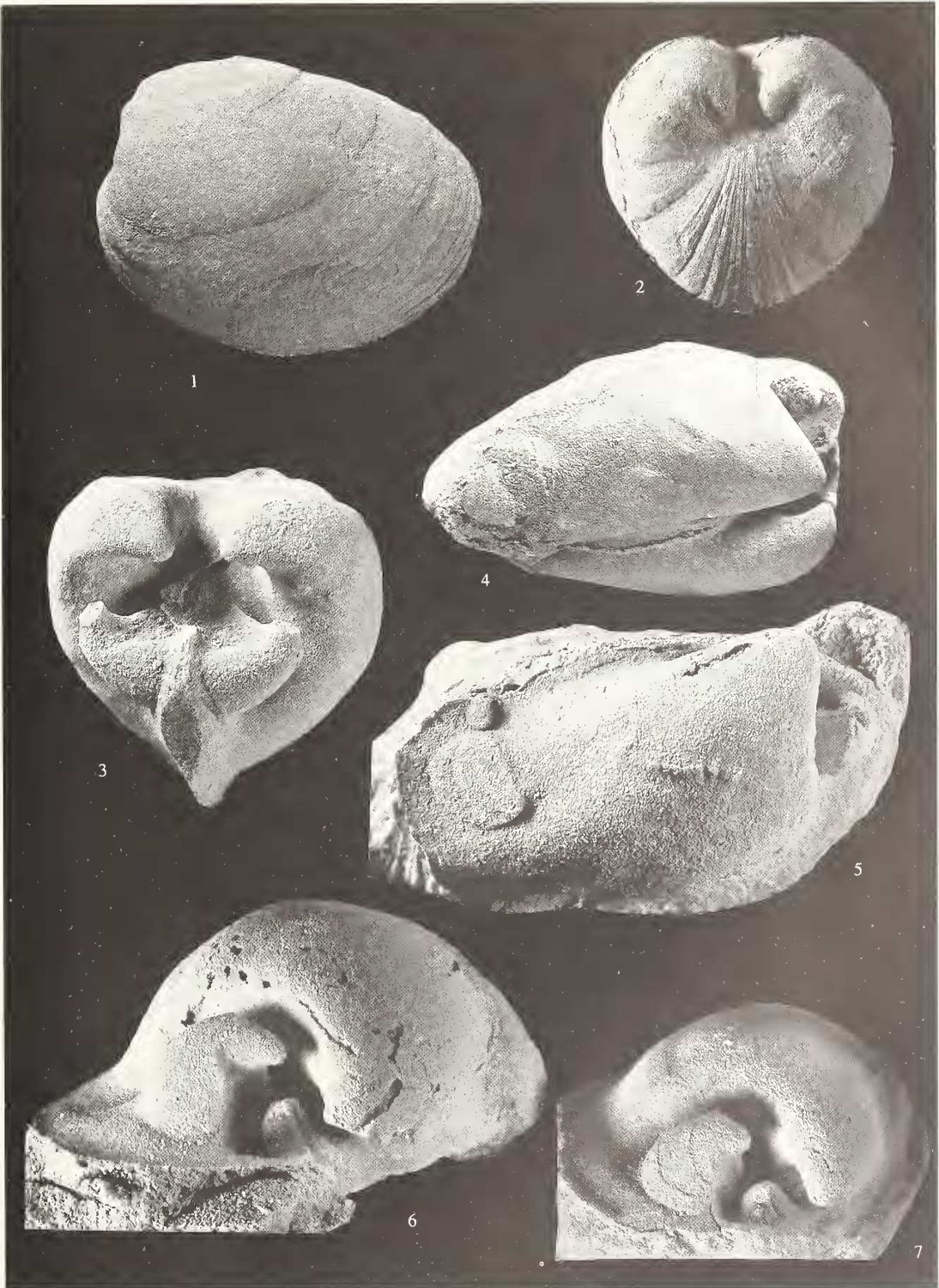
- 1970 *Redonia deshayesi* Rouault, Bradshaw, p. 638, text-figs 16–21.
 1978 *Redonia bohemica* Barrande, Pojeta, pl. 4, figs 1–4.
 non 1978 *Redonia deshayesiana* Rouault, Pojeta, pl. 4, fig. 5 (= *Dulcineaia manchegana* n.g., n.sp.).
 1984a *Redonia deshayesi* Rouault forma α , Gutiérrez-Marco *et al.*, p. 302.
 1984b *Redonia* cf. *deshayesi* Rouault, Gutiérrez-Marco *et al.*, p. 19, pl. 1, figs 13 and 14.



TEXT-FIG. 8. *Redonia deshayesi* Rouault, 1851. Some aspects of the dentition. *a*, latex replica of the left valve of a young specimen (CC-I 2 100/OR), $\times 12$. *b*, dorsal view of the internal mould of the anterior adductor muscle and of the cardinal tooth of a right valve (CC-I 2 087/OR), $\times 5$. *c*, latex replica of the right valve of figure *b*, $\times 5$. *d*, latex replica of the cardinal region of a left valve (RA-I 2 112/OR), $\times 5$.

EXPLANATION OF PLATE 6

Figs 1–7. *Redonia deshayesi* Rouault, 1851. 1 and 2, Luciana (Ciudad Real), middle third of the Navas de Estena Shales, Lower Llanvirn, left and anterior views of a bivalve specimen showing the ornamentation (PI-III 2 125/OR), $\times 3$. 3–7, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 3, anterior view of an internal mould showing two minuscule muscle scars on the anterior part of the left umbonal region (RA-I 2 115^{bis}/OR), $\times 5$; 4, laterocardinal view of an internal bivalve mould showing elongate muscle scars on the umbonal region (RA-I 2 113/OR), $\times 3.5$; 5, internal mould of a right valve showing united small accessory muscle scars (RA-I 2 115/OR), $\times 5$; 6, anterior view of an internal mould of a right valve showing the shapes of the anterior adductor and the anterior tooth (RA-I 2 120/OR), $\times 6$; 7, anterior view of an internal mould of a right valve showing the same morphology and growth lines on the adductor pillar (RA-I 2 117/OR), $\times 6$.

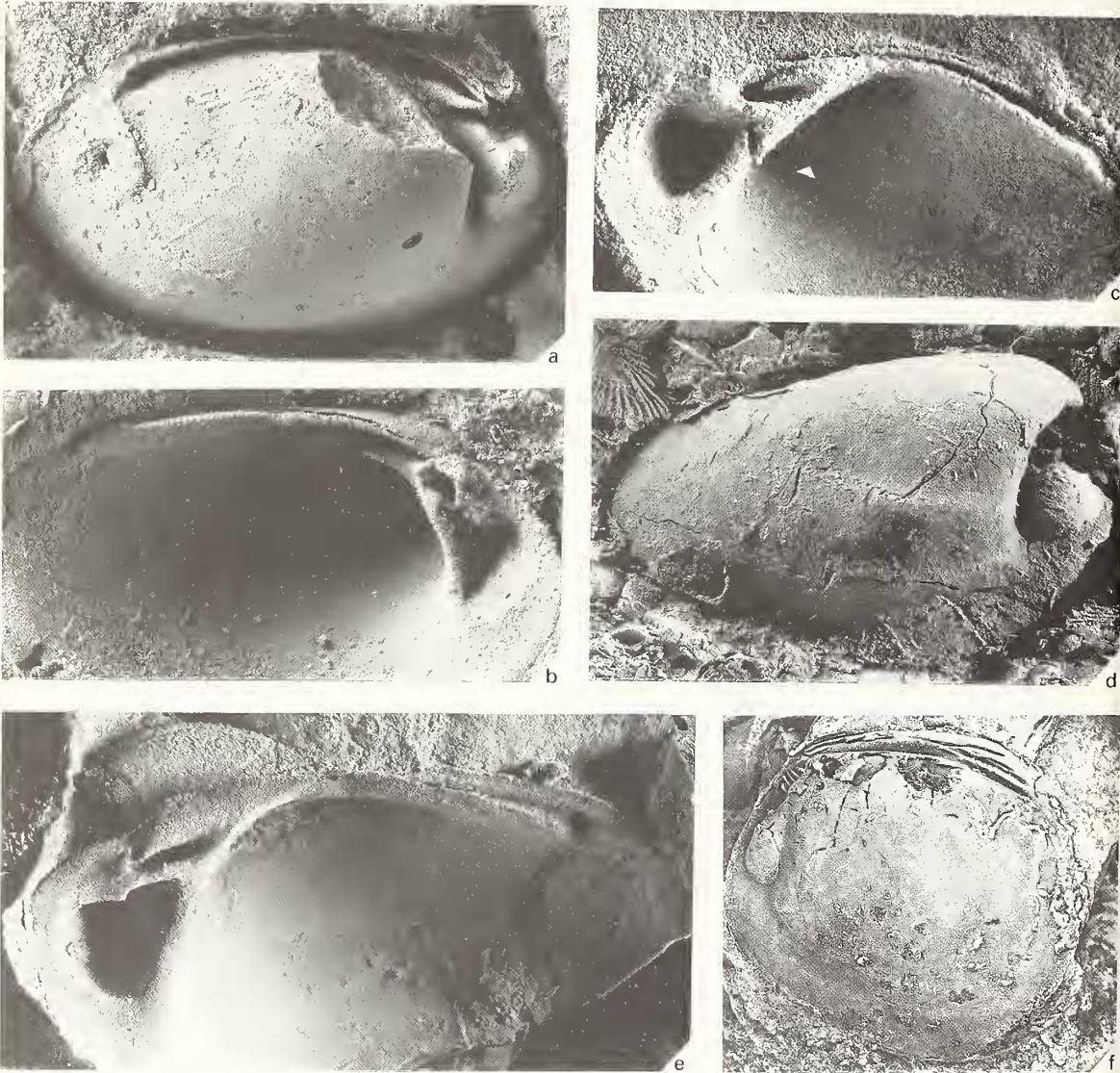


BABIN and GUTIÉRREZ-MARCO, *Redonia deshayesi*

Neotype. LPB 796 (Laboratoire de Paléontologie de Brest). An internal mould of a right valve; Postolonnec Formation. Locality Morgat by Crozon (Finistère, France). Llandeilo (Text-fig. 9*d*).

Material. 825 specimens.

Localities and stratigraphical range. The species is very abundant and reaches a broad distribution (Lower Llanvirn to Upper Llandeilo) in the Tristani beds of the Cantabrian zone (Sueve), West Asturian-Iberian zone



TEXT-FIG. 9. *Redonia deshayesi* Rouault, 1851. Some specimens from other countries. *a*, internal mould of a right valve from Wosck (Bohemia) (FSL 550 120), $\times 5$. *b*, latex replica of a left valve from Postolonnec (Finistère, Armorican Massif) (FSL 550 084), $\times 8$. *c*, latex replica of the right valve of figure *a*, $\times 5$. *d*, neotype, internal mould of a right valve, Postolonnec Formation (Llandeilo), Morgat near Crozon (Finistère, Armorican Massif) (LPB 796), $\times 4$. *e*, latex replica of a right valve from Brix (Armorican Massif), Llandeilo (FSL 550 120), $\times 5$. *f*, *Ananterodonta oretanica* Babin and Gutiérrez-Marco, 1985. Holotype and only known specimen, internal mould of a left valve, San Pablo de los Montes (Toledo), Lower Llanvirn (SP-IV 2 073/OR), $\times 2$.

(TR-III), Iberian Cordillera (CA-II, CR-II, FB-I and IV, HERR-I, PS-I, PO-I), Central Iberian zone (AC-I, ALAM-III, CC-I and III, CHI-I, IV and V, CO-XII and XIV, GS-III, HD-IV-VII, HM-I and IV, LB-I, NE-III-VII, PC-I, PI-II-IV and IX, PSV-II-V, RA-I-VI, RE-IX, SEU-II, SP-IV, SVA-II, VM-I, VPA) and Ossa Morena zone (CS-IV).

Description and discussion. Shell equivalve, strongly inflated and very inequilateral with the umbo anterior and bent on the cardinal line. Ornamentation concentric with some grooves of growth more marked than others (Pl. 6, figs 1 and 2); these may correspond to stasis of annual growth; according to this hypothesis, specimens such as PI-II 2125/OR show that the shell could reach a length of 10 mm during the first year and had slow growth subsequent to the third year.

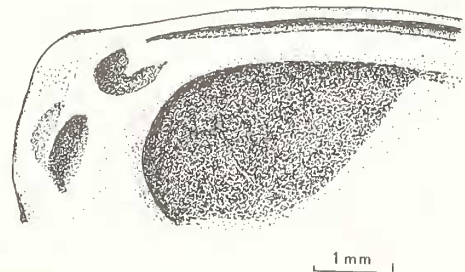
Anterior adductor muscle scar very strongly and deeply impressed with a myophoric plate. Some accessory muscle scars present. A pedal retractor adjacent to the posterior adductor scar; another situated at the internal basis of the anterior adductor (Bradshaw 1970 showed that it corresponds to the fusion of two initially more or less distinct scars). Further accessory scars sometimes visible in the umbonal region. Bradshaw (1970, text-figs 16–20) noted the frequent presence of two scars in this position. In the Spanish material, we can see that these small accessory scars vary in number and shape as is to be expected of individual or populational variation. Specimens from locality RA-I provide good examples of such variability. Some have four small scars which are sometimes united into a single elongate scar (Pl. 6, fig. 5) or which remain separate with an elongate shape directed towards the umbo (Pl. 6, fig 4). One specimen shows in addition two minute scars on the anterior portion of the umbo region (Pl. 6, fig. 3). Pallial line entire.

Dentition very characteristic with pseudolateral and pseudocardinal teeth (Text-fig. 8a–d). On the left valve, a strong pseudocardinal chevron-shaped tooth with an anterior point is flanked by two sockets, the posterior of which, in the concavity of the chevron, is very deep; the two pseudolateral teeth are long and lamellar; one of them begins on the fore part of the hinge plate, the other is thinner, and starts behind the beak; neither is microcrenulated. On the right valve, the plate shows the replicate elements with a pseudocardinal chevron-shaped tooth situated very anteriorly, less developed, and preceding a deep V-shaped socket; the ventral pseudolateral tooth is situated on the edge of the plate; the dorsal pseudolateral tooth is shorter.

This description is of material from the Iberian Peninsula and the Armorican Massif. It agrees too with material from Bohemia designated *Redonia bohémica* by Barrande (1881). Replicas of this species, from the National Museum of Prague sent to us by Dr J. Kríž, show only the posterior part of the lateral teeth. However, in latex moulds of specimens from his own collection (Šárka Formation, Llanvirnian), as he wrote (pers. comm., 1985), 'none of them shows crenulations of the lateral teeth'. We can see, also, that the plate under the umbo, illustrated by Pojeta (1978, pl. 4, fig. 2) is identical to that of *R. deshayesi*. Other specimens from Wosek (Bohemia) given by Barrande to de Verneuil and now housed in Lyon (Text-fig. 9a–c), are sometimes designated *R. deshayesi* and at other times *R. bohémica*. When they cited the occurrence of *R. deshayesi* in Spain, de Verneuil and Barrande (1856, p. 687) added 'cette espèce se trouve aussi dans les schistes du même âge à Vitré, à Gahard, à Monteneuf en Bretagne et en Bohême'. This material exhibits some variation; the Bohemian specimens are smaller than the Breton and Spanish ones, and the internal mould of the anterior adductor is less pointed, although we have intermediates from elsewhere. The dentition, however, is identical with the dorsally very concave small pyramid of the chevron-shaped socket, visible on the internal mould of the right valve (Text-figs 8b and 9a). Thus, we consider all these geographical varieties as conspecific.

R. michelae Babin, 1982, from the Arenigian of the Montagne Noire (South of France) is a distinct species. It is smaller and has a different shape of the anterior adductor; in internal moulds there is a lamellar pillar with a ridged top, perpendicular to the cardinal line; similarly, on the mould, there is a narrow and elongate adductor pit and a large septum, very different from *R. deshayesi*. Nevertheless juveniles of *R. deshayesi* (CC-I 2 212/OR, CC-I 2 213/OR) show a similar morphology (Text-fig. 10) suggesting an evolutionary hypermorphosis for the genus *Redonia*.

TEXT-FIG. 10. *Redonia deshayesi* Rouault, 1851. Umbonal region of the latex replica of a juvenile specimen (CC-I 2 212/OR); the aspect of the muscle scar and of the myophoric plate is very similar to *R. michelae* from Arenig (see Babin *et al.* 1982, pl. 10, fig. 4).



Genus *DULCINEAIA* n. gen.

Derivation of name. Dulcinea, a figure from *Don Quijote de la Mancha*.

Type species. *Dulcineaia manchegana* n. sp. here designated.

Diagnosis. Redoniidae with lamellar and microcrenulated pseudocardinals; elongate pseudolaterals variably microcrenulated.

Dulcineaia manchegana n. sp.

Plate 7, figs 1–8

?1912 *Redonia* Rouault, Douvillé, p. 441, figs 14 and 15.

1978 *Redonia deshayesiana* Rouault, Pojeta, pl. 4, fig. 5.

1984b *Redonia deshayesi* Rouault, forma β , Gutiérrez-Marco *et al.*, p. 302.

Holotype. Internal mould of a right valve showing the dentition, CC-I 2 140/OR.

Type locality and horizon. SE of Calzada de Calatrava (Ciudad Real), 70 m S of the km 47,500 of C-410 highway, just at the dam base of the Fresneda reservoir, right bank. Middle part of the Guindo Shales, late Lower Llandeilo (top of the Tournemini Biozone).

Derivation of name. After La Mancha region, Don Quixote's country, near to which important Ordovician fossil localities are located.

Paratypes. CC-I 2 074/OR-2 077/OR, 2 084/OR, 2 088/OR, 2 090/OR, 2 094/OR, 2 097/OR, 2 110/OR, 2 126/OR, 2 139/OR; PZ-III 2 102/OR-2 107/OR, 2 193-2195/OR; RA-I 2 109/OR, 2 111/OR, 2 119/OR, 2 126/OR; RE-VII 2 108/OR.

Diagnosis. As for genus.

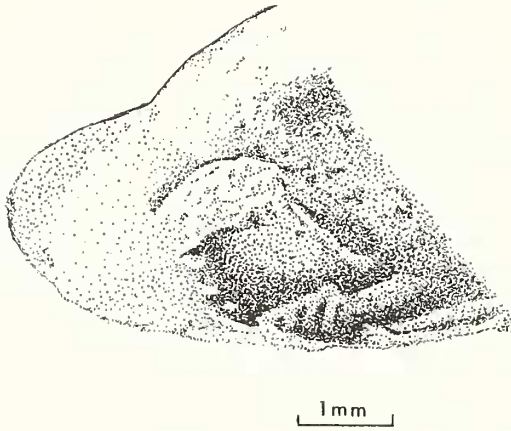
Description and discussion. Shell equivalve, with an oval outline and strongly inequilateral with the umbo at the anterior. This morphology is similar to *R. deshayesi* and the two species are not distinguishable by their shapes. Posterior adductor muscle scar oval, large, placed under the end of the hinge plate, and weakly impressed. A small pedal retractor lies above it. Two other accessory scars are sometimes observed in the umbonal region of the shell; one is situated in front of the adductor, at one third of the distance to the beak, the other, smaller one is at half of that distance (Pl. 7, fig. 4). The anterior adductor scar is deeply impressed and corresponds, on the internal moulds, to a strong pillar, as in *R. deshayesi*. However, the shape of the pillar is a little different; the point, generally more obtuse, is rather more oriented towards the anterodorsal angle of the valve and its upper face is less strongly concave than in *R. deshayesi*. This morphology, combined with the differences of the pseudocardinal tooth, distinguish the two species in the internal moulds (the most common material) when observed by their anterior side and even if the microcrenulations of the teeth cannot

EXPLANATION OF PLATE 7

Figs 1–8. *Dulcineaia manchegana* n. gen., n.sp. 1, 3–8, Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo. 1, holotype, internal mould of a right valve (CC-I 2 140/OR), $\times 4$; 3, paratype, internal mould of a right valve accompanied by a right valve of *Myoplusia* (CC-I 076/OR), $\times 3$; 4, dorsal view of internal mould of a right valve showing the microcrenulations on a tooth and accessory muscle scars (CC-I 2 110/OR), $\times 8$; 5, latex replica of the same specimen, $\times 9$; 6, paratype, latex replica of a right valve showing the dentition; 7, internal mould of a left valve (CC-I 2 097/OR), $\times 2.8$; latex replica of the same specimen, $\times 4$. 2, Pozuelos de Calatrava (Ciudad Real), Valdemosillo Shales, Upper Llandeilo. Detail of the microcrenulated anterior tooth on the left valve of a relatively young specimen: latex replica (PZ-III 2 105/OR), $\times 8$.



BABIN and GUTIÉRREZ-MARCO, *Dulcineaia manchegana* n.gen., n.sp.



TEXT-FIG. 11. *Dulcineaia manchegana* n.g. n.sp. Anterior dorsal region of the internal mould of a right valve (CC-I 2 076/OR) showing the microcrenulations on the tooth and three minute scars between the adductor pit and this tooth.

be seen. Some specimens show a series of minute scars (2–5) on the basal part of the anterior adductor (Text-fig. 11).

The dentition of *D. manchegana* is distinctive. The left valve shows a short lamellar tooth, situated under the umbo in a ventral position and directly bordering the deep adductor scar. The faces of this tooth are microcrenulated during early ontogeny (Pl. 7, fig. 2); it ends posteriorly near the myophoric buttress. A long, pseudolateral tooth, begins at the fore part of the shell, at about the same place as the ventral tooth; it is generally microcrenulated in its anterior region and, sometimes for up to 3/4 of its length (for example the paratype CC-I 2 097/OR).

The systematic position of *Dulcineaia* is not clear. We place it tentatively in the Redoniidae but the microcrenulations of the teeth pose a problem. Another genus with crenulated teeth, *Noradonta* Pojeta and Gilbert-Tomlinson, 1977, has been included in the Lyrodesmatidae, and Babin (1982) has referred to it a species from the Arenig, *N. redoniaeformis* (Thorl), which has a similar morphology (the type-species, *N. shergoldi*, also has a deeply impressed anterior adductor muscle). However, the species of *Noradonta* have several anterior teeth below the beak which more or less radiate from it; moreover the posterior elongate teeth are strongly crenulated. On the other hand, *Dulcineaia* has only one or two teeth beneath the umbo which are parallel to the dorsal margin of the shell; and like the pseudolaterals, they are slightly microcrenulated for part of their length or even entirely smooth. We suggest this species is allied to *Redonia* but it is clear that the differences between these genera are becoming less conspicuous with the new discoveries.

Finally, it is interesting to note that the stratigraphic distribution of *D. manchegana* is more restricted than that of *R. deshayesi*. The latter is known from the Llanvirn (Armorican Massif, Bohemia, Portugal, Spain, Morocco) and it continues in the Lower Llandeilo even when *D. manchegana* appears (the two species are present simultaneously in locality CC-I). Afterwards *D. manchegana* seems to remain alone in Upper Llandeilo levels together with the trilobites *Placoparia borni*. In this way, *D. manchegana* could be an index fossil but its geographic extension may have been restricted. In the literature, Douvillé (1912, p. 441) has figured two valves of *Redonia*, the dentition of which suggests that they belong to *D. manchegana*. This material came from the Ordovician of Brix (Normandy) and is in the collections of the Ecole des Mines (Paris), at present in Lyon. We have found in these collections two right valves from the same locality (and probably from the Moitiers d'Allonne Formation) and they are exactly determined *R. deshayesi* by the shape of the teeth without microcrenulations (Text-fig. 9e). So, the observation of Douvillé remains enigmatic. On the other hand, we have found in de Verneuil's collections, in Lyon, some poor but interesting specimens from Vitré (Brittany); the morphology of the anterior adductor and the visible part of the dentition show that they do not belong to *R. deshayesi*; they may in fact be *D. manchegana*.

SOME THOUGHTS ON EARLY ORDOVICIAN BIVALVE PHYLOGENY

'The strength of any phylogenetic hypothesis must be found in its corroboration by disparate data sets' (Laws and Fastovsky 1987). Among these data sets, morphology and stratigraphic

superposition are both incomplete but their 'value and significance in phylogeny reconstruction are unquestionable'. With these remarks in mind, what can we attempt with respect to Ordovician bivalve phylogeny? The present material from the Middle Ordovician is interesting because in the Llanvirn a marked explosion of diversity of bivalve faunas occurs.

After the first known minute bivalves (Fordillidae) from the Lower Cambrian, the pelecypods remain very poorly known from the Middle and Upper Cambrian and during the Tremadoc, with only five or six species worldwide (Pojeta 1985; Pojeta and Runnegar 1985) and the age of some of these, like *Afghanosdesma* (Desparmet *et al.* 1971), is uncertain. The faunas from the Arenig are also geographically restricted despite some radiation. During the Llanvirn, the diversity of the faunas increases, but they are dominated by palaeotaxodontids and actinodontids. The phyletic relations of these two groups remain obscure. In the opinion of Douvillé (1912), Babin (1966), Morris and Fortey (1976), and Morris (1978), the actinodont type was probably the more primitive. Pojeta (1978) expresses doubt about this after the description by Allen and Sanders (1973) of the curious living deep-sea protobranch *Praelametila* and he concludes 'which group gave rise to the other is not clear'. Since the recent study on *Pojetaia* and its earlier appearance (Pojeta 1985), Pojeta and Runnegar (1985) admit that the heteroconchs might be descended from the paleotaxodontids; the latter are considered as occurring earlier, but this needs confirmation, in particular from the fauna described by Harrington (1938) from Argentina. It seems that 'during the Lower Ordovician, nuculoids are not so well represented as the Cycloconchacea' (Morris 1978). In contrast, during the Middle Ordovician, paleotaxodontids appear more diversified. Praenuculidae with an elongate anterior end become abundant. *Cardiolaria*, with resorption during ontogeny of the umbonal teeth, might 'indicate a very early stage in the migration of the external ligament onto the hinge plate' (Bradshaw 1970). *Ekaterodonta hesperica* is a Llanvirn species of this genus originally described from the Arenig of the Montagne Noire (Babin 1982) and which is related to another Llanvirnian genus from Spitzbergen, *Tirouucula* Morris and Fortey, 1976. The potential phyletic interest of these forms is to show the possible evolution of a pseudolateral tooth 'by extending one arm of the V (of a chevron tooth) and suppressing the other', as described by Allen and Hannah (1986) with regard to the Recent and conservative Lametilidae and Siliculidae. The arrangement of the pedal muscles of the Ordovician paleotaxodontids is also primitive (cf. *Myophusia*) and is later modified in the Upper Palaeozoic protobranchs (Driscoll 1964).

However, in the actinodontids, the diverse arrangements of the teeth justify the taxonomic discrimination of several genera, even though some of them are monospecific, and there is a rapid diversification. The relationships between them remain imprecise because of the durations of these stages (about 20 My for Llanvirn and Llandeilo together, after Odin 1985) and the incomplete biostratigraphical record. In addition, we are not able, on the present data, to decide on ancestral and derived characteristics in the arrangement and structures of the teeth. Thus, we cannot suggest precise phyletic relationships other than to underline some particularities of the species described above.

The dentition of *Ananterodonta*, known from a single specimen, resembles that of the living solemyoid *Nucinella* of which Allen and Sanders (1969) said 'it should be considered as a rather specialized member of the Actinodonta'. This remarkable fossil, may give us an indication of the pteronch Cyrtodontidae in the trend of reduction of the anterior part of the posterior pseudolaterals.

Another problem concerns the relationships between actinodontids with and without microcrenulations on the teeth. A review of the presence of microcrenulations in diverse Palaeozoic bivalve groups, to compare with the ontogeny of living pelecypods, has been made by Babin and Le Pennec (1982). Microcrenulations are known from the Upper Tremadoc and the Arenig in *Babiinka* and lyrodesmatids like *Tromelinodonta* and *Noradonta*. The discovery of *Dulcineaia* poses the problem of the relationships of this genus with *Redonia*, and others. Formerly, it was considered that 'it is highly likely that *Redonia* developed from a form with a dental plate similar to that of *Actinodonta*. The fusion of the teeth in both forms follows a similar pattern but has been more extreme in *Redonia*' (Bradshaw 1970), following research on *Actinodonta naranjoana*

(= *Glyptarca ? lusitanica*). It appears that *Redonia* was derived from a primitive actinodontid, but it is not a descendant of *Glyptarca?* which appeared later. Morris and Fortey (1976) granted particular phyletic importance to the microcrenulations, suggesting 'that the origin of the posterior hinge teeth in the Nuculoida... is by the breakup of originally radiating "actinodont" teeth by enlargement of their transverse ridges'. Nevertheless, microcrenulations appeared independently several times; early (Upper Tremadoc-Lower Arenig) in *Babinka* and Iyrodematids, and later (Upper Llanvirn-Llandeilo) in cycloconchids with the single genus *Glyptarca ? lusitanica*. There, only the posterior pseudolaterals are microcrenulated; this phenomenon appears early during ontogeny but the microcrenulations are less developed than forms like *Noradonta*. By contrast, *Glyptarca?* seems to be a cycloconchid acquiring crenulations rather than a Iyrodematid reducing them. We have shown that a specimen from the Upper Llandeilo (Text-fig. 6f) has crenulations on its anterior tooth. As it is not apparently a senile avatar, was it a teratological feature or a prophetic one without continuation because of the disappearance of the genus?

Still more curious and obscure are the relationships between *Redonia* and *Dulcineaia*. The former is known, in its typical morphology (*Redonia michelae*), as early as the Lower Arenig from the Montagne Noire. It remained without notable changes during the Llanvirn and the Lower Llandeilo (*R. deshayesi*); suddenly, during the Llandeilo, the genus *Dulcineaia* appears with a very similar morphology to *Redonia* but with different cardinal teeth. Are they only homeomorphs or are they really related? We have preferred the latter alternative and placed *Dulcineaia* among Redoniidae. Is it an atavic reappearance of an ancestral form and how did it occur? Is it a true innovation, i.e. a case of divergence? This phenotypic novelty certainly did not appear as a response to new constraints, since *Redonia* and *Dulcineaia* lived together, in a similar habitat and we do not see structural modifications either of the whole shell or of the hinge plate. Unfortunately, we are not in a position to compare the ontogenies of the two genera. The mode of bivalve preservation as internal moulds is not suitable for the examination of very minute specimens. Finally, we have a young specimen (CC-I 2 100/bis/OR; right valve) showing a socket followed by a bud, but we cannot assign it to either of the genera because they coexist in the locality; the juveniles are possibly indistinguishable.

We should bear in mind, as with the microcrenulations, that the trend towards production of crenulated teeth is common among actinodontids and their descendants. Later, a similar feature occurs in the Devonian genus *Tanaodon* Kirk, considered by Pojeta and Runnegar (1985) to be 'a late surviving actinodontoid'. Heidecker (1959) has figured strong microcrenulations in *Neoactinodonta*, which is considered a junior synonym of *Tanaodon* and so, in the Treatise, *Tanaodon* is defined as 'with or without cross striations' on the teeth. This however is probably a character without important taxonomic significance and therefore we can place *Glyptarca?* in the Cycloconchidae and *Dulcineaia* in the Redoniidae. Still more surprising is the development of crenulations on the teeth among paleotaxodontids, like some *Nuculites* during the Devonian (Babin 1966). In such cases, the teeth beneath the umbo also show stronger crenulations than the posterior ones. The function of these microcrenulations is not clear, because, according to Allen and Hannah (1986), 'the nuculoid tooth in multiple array forms an incredibly strong hinge and in some species it is impossible to open the shell wide without shearing the teeth'. *Nuculites* has a myophoric buttress, also a character of *Dulcineaia* and *Noradonta*, but with a different orientation in relation to the hinge margin. In the actinodontids the microcrenulations restrict movement forwards and backwards and in the palaeotaxodontids they restrict dorsoventral sliding. There do not seem to be any general constraints governing the evolution of microcrenulations in bivalves.

THE PALAEOECOLOGY AND PALAEOGEOGRAPHICAL SIGNIFICANCE OF THE MIDDLE ORDOVICIAN BIVALVE FAUNAS

Since a subsequent paper will include detailed palaeoecological analysis of these formations, our treatment here is brief. There is, in this area, a relative stability in composition of the benthic assemblages, with bivalves, brachiopods, trilobites, echinoderms and ostracodes co-occurring for

some 10 to 15 My; thus the trophic structure evidently remained nearly the same for a long time. In these assemblages the bivalves are mostly shallow-burrowing, with deposit feeders the dominant trophic group and with small body sizes. Like Frey (1987a), we tabulate here the mode of life of the observed genera (Table 1).

TABLE 1.

Genera	Mode of life
Palaeotaxodonta	
<i>Praenucula</i>	infaunal deposit feeder
<i>Ekaterodonta</i>	infaunal deposit feeder
<i>Myoplusia</i>	infaunal deposit feeder
<i>Cardiolaria</i>	infaunal deposit feeder
Heteroconchia	
<i>Babinka</i>	shallow infaunal filter feeder
<i>Coxiconcha</i>	shallow infaunal filter feeder
<i>Glyptarca?</i>	shallow infaunal filter feeder
<i>Redonia</i>	shallow infaunal filter feeder
<i>Ananterodonta</i>	shallow infaunal filter feeder
Pteriomorpha	
<i>Cyrtodontula</i>	endobysate filter feeder
Isofilibranchia	
' <i>Modiolopsis</i> '	endobysate filter feeder

After the first minute bivalves of the Cambrian, a progressive increase in size characterizes the Ordovician diversification. There is some variation according to environment. During the Arenig, for example, bivalves are large but are very scarce in the Armorican Sandstone, while they are numerous and small in the muds and sandy muds of the Montagne Noire. In the muddy Middle Ordovician facies of the southern Perigondwanan platform, they are generally small, with some exceptions like *Cadomia* and *Coxiconcha* or, occasionally, with individual gigantism (we have one specimen some 60 mm long). During the Late Ordovician, it seems that there is a further increase in size. Most of the studied faunas came from mudstones and siltstones. All these burrowing forms lived in soft sediments, mainly muds or muddy silts. Several were very shallow burrowers. Two specimens of *Glyptarca?* (FO 2 135/OR and CC-I 2 208/OR) and one of *Redonia* (CC-I 2 211/OR), for example, show a bryozoan incrustation (Pl. 6, fig. 1) suggesting that this part of the shell projected above the sediment-water interface; this attitude is similar to that figured by Frey (1987a, fig. 7) for *Cyrtodontula sterlingensis* which is a homeomorph of *Glyptarca?* Two specimens of *Praenucula sharpei* show small pits on the ventral part (Pl. 1, figs 5 and 6); identical pits in a pallial position occur in a specimen of the same species from the Armorican Massif (FSL 550 091).

Comparing localities, at La Vibora (the fossils were collected by P. Rossi about 1974), the facies is a fine shallow-water sandstone; the coquina is composed mostly of bivalves; among 177 fossils, there are 167 bivalves (94% of the fauna), 2 rostroconchs (*Ribeiria*), and 8 brachiopods (*Heterorthina*). The bivalves are *Praenucula costae* (43.7%), *Cardiolaria beirensis* (27.5%), *Glyptarca? lusitanica* (21.6%), and small undetermined paleotaxodontids (7.2%). The age is probably Upper Llandeilo, and this may explain the absence of *Redonia*, but other forms known in these levels, such as *Dulcineaia manchegana* and *Myoplusia bilunata*, also seem to be lacking. Among our localities, a deeper water bivalve assemblage is apparently provided by site CR II, a black muddy facies with an undisturbed assemblage of numerous small specimens of *Redonia deshayesi* and other species such as *Ekaterodonta hesperica*, *Goniophora* sp., and cf. *Ctenodonta escosurae*. We consider this locality as corresponding to the offshore shelf. Therefore, we agree with

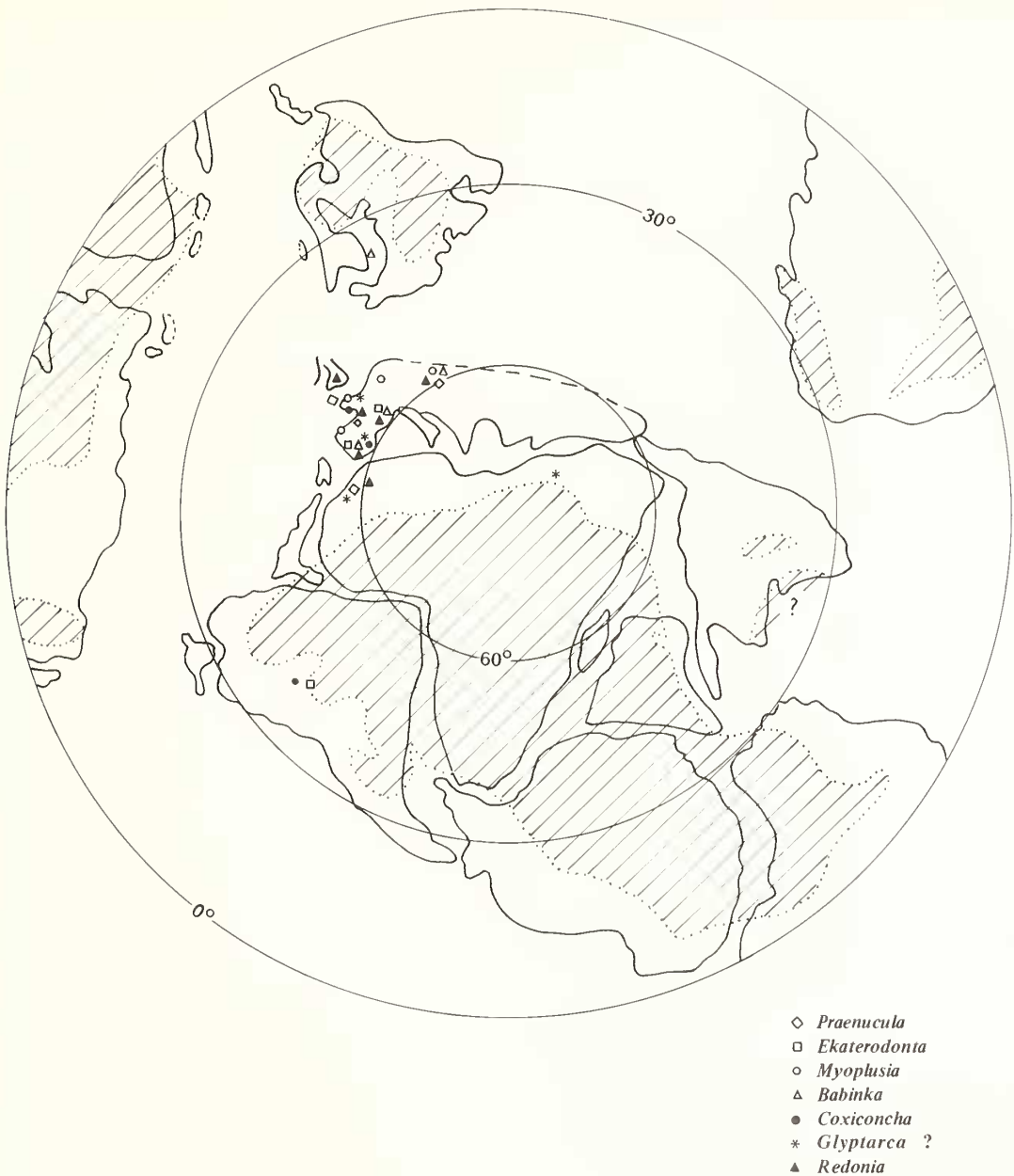
Morris (1978) that as early as the Lower and Middle Ordovician, some bivalves inhabited this part of the shelf in western Europe, while in North America (Frey 1987*a, b*) the first intrusions into offshore shelf environments by pelecypods occurred only during the Late Ordovician. It is worth noting that among the fauna of this locality the genus *Ekatereodonta* occurs, described from the Arenig of the Montagne Noire (Babin, 1982) and which appeared here as a conservative form in the deeper water habitats.

Finally, we can attempt to consider the spatio-temporal distribution of these faunas, their relationships with the ancestral Arenig stocks, and we can attempt to evaluate migrations and their causes. Before plate tectonic reconstructions, Spjeldnaes (1961) correlated Ordovician faunal provinces with climatic zones. Several palaeogeographic reconstructions have been produced during the last fifteen years. Bouyx (1988) has compared these different reconstructions; some of them, like that of Smith (1981) appear inconsistent with the data on facies and faunas. Most of them agree roughly with that of Text-figure 12 as regards the southern hemisphere during the Early Ordovician.

The distribution of bivalve faunas has rarely been considered, though since they are benthic they are worth including. A comprehensive worldwide comparison, however, still requires many investigations. Numerous regions are poorly documented and new studies can bring important fresh data (see for Australia, Pojeta and Gilbert-Tomlinson 1977, or for Bolivia, Babin and Branisa 1987).

The present area belongs to the *Selenopeltis* trilobite province of Whittington and Hughes (1972) and, more interesting for facies control, our faunas belong to the characteristic assemblages of fossils termed the *Neseuretus* community type by Fortey and Owens (1978), a community considered to have been shallow-water and inshore in clastic facies. A cool environment is inferred from the latitudinal position of the *Neseuretus* community. In this reconstruction, the postulated Proto-Tethys of Whittington and Hughes (1972) is abandoned; high palaeolatitudes from France and Iberia were confirmed recently by palaeomagnetic data (Burrett 1983). Nevertheless, Hallam (1984) reminds us that eustatic events 'were in general more significant than temperature' in controlling faunal provinciality. With the revival of interest in global changes of sea level (Vail *et al.* 1977), Fortey (1984) has examined the biological implications of these changes during the Ordovician; he gave a sea level curve for Tremadoc to Caradoc with an important regressive-transgressive event at the Arenig-Llanvirn boundary and another one during the Llandeilo; this postulated global eustatic curve is shown more precisely in Fortey and Cocks (1986).

The relationships of the southern Gondwanan shelf to other parts of Europe have also recently been discussed. Whittington (1963) postulated a marine barrier between Gondwana and Baltica (see also Babin *et al.* 1980), but its dimensions were probably not important (Bouyx 1988); this was recently named Tornquist's sea by Cocks and Fortey (1988). The detailed palaeogeography of the Gondwana platform itself during the Lower and Middle Ordovician is not clearly established. Several areas appear distinctive, and Cocks and Fortey (1988) suggested 'a deeper water tongue between Armorica and Iberia running from the region of Ancenis, Brittany to the Montagne Noire in Southern France'. The Ossa Morena Zone in southern Spain is also anomalous. The Spanish faunas tell us that extension of the range of bivalves was caused by the widespread Llanvirnian transgression. But the Ordovician radiation for example (Sepkoski 1979) took place in the pelecypods of the Perigondwanan area during the Arenig rather than 'in the transition from the Lower to Middle Paleozoic' period of increase for marine benthic faunas (Bambach 1977). We do not know where the diversification of the bivalve communities took place in the Perigondwanan ring. During the Arenig, pelecypods are cited at low latitudes (Argentina, Australia) and at higher latitudes (Montagne Noire, Armorican Massif, Wales). The poor correlations between these areas do not permit determination of the thermal preferences of the primitive bivalve populations. On the southern Gondwanan shelf in the Montagne Noire, corresponding to the 'deeper water tongue' on the platform, pelecypods are known as early as the Late Tremadoc (*Babinka*) and then diversified during the Lower Arenig (*Babinka*, *Redonia*, *Synek*, *Thoralia*, *Noradonta*, *Coxiconcha*, *Ekatereodonta*); they inhabited fine sediments and probably cool waters. This area could have been the place of origin of several genera. During the Upper Arenig, some pelecypods of larger size colonized



TEXT-FIG. 12. Distribution of some bivalve genera during Arenig (Montagne Noire) and Llanvirn-Llandeilo (other countries) on the Perigondwanan platform. Palaeogeographic reconstruction after Gutiérrez-Marco and Rábano (1987); land areas are shaded. See also Cocks and Fortey (1988) for biofacies distribution around Gondwana.

shallow-water sands like those of the Armorican Sandstone, with actinodontids, lyrodesmatids (*Tromelinodonta*), and scarce palaeotaxodontids (*Praenucula oehlerti*). The rapid expansion of the Llanvirn is not uniform and, during the whole Middle Ordovician, the reasons for particular distributions and migrations remain obscure. Among the palaeotaxodontids, which often constitute

the dominant element, the genus *Praenucula* is common in the Ibero-Armorican province as well as Morocco, Bohemia or on the marginal edge of the shelf (e.g. Ardenne) but the species are not determined with certainty and it is difficult to follow the possible migrations. The case of *Ekaterodonta* is peculiar. This genus, known in the Arenig from the Montagne Noire, appears like a relict in some deeper facies during the Llanvirn from the Hesperian Massif but it is present at the same time in Bolivia at a lower latitude, and the first described Tironuculidae, *Tironucula*, is a contemporaneous form from the Laurentian platform. During the Llandeilo, *Myophusia bilunata* existed in Brittany and Spain (and perhaps in the Ardenne?); and persisted into the Caradoc in the Armorican Massif and Bohemia. But another common Ibero-Armorican species, *Cardiolaria beirensis*, is unknown elsewhere. Still more curious, *Tancrediopsis ezquerrae*, a common form in Portugal and Brittany, remains to be found in the Spanish area.

If we compare the palaeotaxodontids from other areas of the world, we can see a sudden diversification during the Llanvirn in varied facies from lower latitudes (North America, Baltica, Australia, South America). In these regions there are representatives of *Ctenodonta* and *Deceptrix* but also there are often numerous genera unknown in the Ibero-Armorican region, like *Similodonta?* in Norway (Soot-Ryen and Soot-Ryen 1960) or the various genera described from Australia, such as *Eritropis* and *Johumartinia*, which are frequently found in sandstones (Pojeta and Gilbert-Tomlinson 1977).

The isofilibranchs and pteriomorphids are scarce in the Ibero-Armorican area; but they are more frequent and diversified in Baltica (Soot-Ryen and Soot-Ryen 1960) in the more calcareous facies and warmer waters.

The actinodontids and their problematic allied genera, *Babinka* and *Coxiconcha*, are also interesting in their spatio-temporal distributions. *Babinka prima* appears early in the Upper Tremadoc in the Montagne Noire and it remains until the Upper Arenig in this region where post-Arenig rocks are unknown. During the Llanvirn, the same species occurs in Bohemia and in the Hesperian Massif, but it remains unknown among similar communities and environments in Portugal and in the Armorican Massif. On the other hand, *B. oehlilandica* was described by Soot-Ryen (1969) from Baltica around the Arenig-Llanvirn boundary. Thus, from the Montagne Noire, *Babinka* migrated to some sites on the southern Gondwanan shelf without recognizable specific variation during a time interval of about 20 My and it crossed Tornquist's sea to reach the Baltica shelf, giving rise to another species. *Coxiconcha* is also known from the Montagne Noire as early as the Lower Arenig and remained there during the whole stage. During the Llanvirn and Llandeilo, the genus was abundant, with a larger species *C. britannica*, in the muddy sea floors of the Ibero-Armorican area and it migrated along the Gondwanan coast giving another species in Bolivia. However, it remains unknown from Bohemia.

Among the Cycloconchidae, *Glyptarca* ? is a genus with a widespread distribution on the southern Gondwanan shelf. Originally described from Portugal, it is common from the Middle Ordovician in the whole Ibero-Armorican province, usually in muds, but sometimes adapted to sandy sediments. *Glyptarca* is cited from Saudi Arabia (Fortey and Morris 1982) and may occur in Morocco (Babin unpublished) but is unknown from Bohemia (Born 1918). Finally, the Redoniidae present other differences. The first known *Redonia*, *R. michelae*, is known from the Montagne Noire, as early as the Lower Arenig. Like the other bivalves from these environments, relatively deep on the platform, this species is a small one. In the Armorican Sandstone, from the Upper Arenig, the poorly known *R. boblayei* (Barrois 1891) is larger. During the Llanvirn, *Redonia deshayesi* is an important element of the benthic Ibero-Armorican communities. It is also present in Bohemia in similar environments and in Morocco in sandy facies. The genus was cited as *R. anglica* in Shropshire by Salter (1866). *Redonia* appears to have been eurytopic with regard to grain-size but was probably a stenotherm, preferring cold water. We can thus explain its presence in the deeper zones of the platform (Montagne Noire during the Arenig; locality CR II in the Hesperian Massif and occurrence in the Ossa Morena Zone during the Llanvirn) as in the higher latitudes (Morocco). Around Gondwanaland *Redonia* is unknown from South America or Australia, where it was erroneously cited by Warris (1967) (after Pojeta and Gilbert-Tomlinson 1977). The new genus *Dulcineaia* is known only from the Llandeilo of the Hesperian Massif.

In conclusion, this study of Spanish bivalve faunas underlines the necessity for further new investigations. Bivalve distribution is apparently complex, with some endemics. To confirm this, more data are needed from the Ibero-Armorican area, the Bohemia faunas require revision, and the Moroccan ones need to be studied. As Boucot (1985) has stated 'the pelecypods are a group deserving a great deal more taxonomic attention and collecting before one can be certain of such conclusions'.

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